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## Evaluation of heterotic patterns between Stiff-Stalk and Non-Stiff Stalk maize populations based on Design II crosses

Christopher Cole Rasmussen  
*Iowa State University*

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**Evaluation of heterotic patterns between Stiff-Stalk and Non-Stiff-Stalk maize  
populations based on Design II crosses**

by

**Christopher Cole Rasmussen**

A thesis submitted to the graduate faculty  
in partial fulfillment of the requirements for the degree of  
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Program of Study Committee:  
Arnel R. Hallauer (Major Professor)  
Arden Campbell  
Philip Dixon

Iowa State University  
Ames, Iowa

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Graduate College  
Iowa State University

This is to certify that the master's thesis of

Christopher Cole Rasmussen

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

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## INTRODUCTION

Significant scientific contributions toward the development of the modern heterosis concept in many crop species were first observed by the early plant breeders in the late 18<sup>th</sup> and early 19<sup>th</sup> centuries. At this time, much of their work was concerned more with the results of divergent cross experimentation rather than emphasis on practical plant improvement (Mayr, 1982). However, the detailed results from their divergent cross studies, indicating the observance of hybrid vigor, or *heterosis*, following cross-pollination, caused later plant researchers to consider plant hybridization further.

In maize (*Zea mays* L.), plant hybridization was first observed by Charles Darwin, who experimented with the reproductive modes of maize through inbreeding (self-pollination) and outbreeding (cross-pollination). Darwin reported the results following outbreeding of 37 crosses, which included maize crosses, where he observed increased height in 24 crosses (Goldman, 1997). Darwin's results also recognized that self-pollinated plants had reduced plant size compared with outbred plants, but this reduced plant size could be increased following outbreeding.

In the late 19<sup>th</sup> century, William James Beal, who was aware of Darwin's results, conducted an experiment that is analogous to present-day methods for maize hybridization on a large-scale basis (Hallauer and Miranda, 1988). Beal's study focused on pollination control and variety crossing by producing hybrids between different open-pollinated varieties. Although Beal did not give detailed results, Beal stated that the yields of the hybrids were larger than those of the parents by as much as 40% (Allard, 1960). Future plant breeders, impressed by Beal's results, also recognized the potential benefits of variety crossing and heterosis upon utilizing divergent parental stocks in crosses to help develop hybrids with increased grain yields.

During the first two decades of the 20<sup>th</sup> century, plant breeders developed and tested crosses between open-pollinated varieties, but Richey (1922) stated there were not consistent advantages between the cultivars themselves and their crosses. Genetic variability within cultivars, sampling technique, and cultivar testing methods also contributed to the failure to demonstrate that cultivar crosses were consistently better than cultivar *per se* performance

(Hallauer, 1990). With the role of hybridization being developed, attention was turned to trying to understand the effects of inbreeding for the production of inbred lines.

The use of inbreeding within germplasm populations or cultivars for production of inbred lines was utilized in the pure-line/hybrid breeding method developed by Shull (1908, 1909, 1910). Shull's pure-line method allowed breeders a way to maximize heterotic response between inbred lines developed from the genetic variability present within different germplasm populations. However, even though the pure-line method of maize breeding was suggested in 1909, it was not until the 1930's that maize hybrids in the form of double-crosses started to become available to producers.

Even with plant breeders starting to realize the ability of capturing heterosis in crosses between inbred-lines, the genetic mechanism of how heterosis was expressed upon crossing remained unknown. Different theories had been proposed to explain heterosis, some having a genetic basis and some not having a genetic basis, but most could be included into either one of the two following categories: a) physiological stimulation (allelic interaction or overdominance) and b) dominant favorable growth factors (Hallauer and Miranda, 1988). Today, plant breeders have generally accepted the dominance theory for the genetic explanation of heterosis; however, acceptance of the dominance theory was not true 50 years ago (Labate *et al.*, 1997).

During the 1930's, with the genetic basis of heterosis under study, improved inbred lines and hybrids came from the management of different germplasm sources. Germplasm sources for extraction of inbred lines had changed from the use of open-pollinated cultivars to pedigree selection within  $F_2$  populations of elite line crosses (Jenkins, 1978). The recycling of elite inbred lines had shown consistent, incremental improvements throughout time. Cross performance of elite lines also helped identify the possible heterotic group relationships in which the inbred line, variety, or population belonged to. Simultaneously, the idea of maternal inheritance in traits such as grain yield was also evaluated to help determine proper heterotic group classification. Phenotypic plant characteristics of some populations (*i.e.*, medium-sized ear, larger number of kernels) allowed better performance as a female parent in crosses verses their use as a male parent or vice versa which led to a population's placement into a heterotic group having the same similarities. Currently plant

breeders do not place much emphasis on maternal effects or reciprocal effects when characterizing populations *per se* or their population crosses based on agronomic trait performance. Therefore heterotic groups and their patterns generally represent broad, but distinct sources of germplasm that plant breeders utilize to maximize heterotic response (*i.e.*, Reid Yellow Dent – Lancaster Sure Crop; U.S. Dents – European Dents). The consequence of line recycling, however, was the loss of genetic variability that occurred with each successive recycling of elite lines.

Most of the maize hybrids used in the U.S. Corn Belt are produced from inbred lines that represent a relatively narrow germplasm base (Smith, 1988). Many plant breeders have expressed concern toward the need to integrate exotic germplasm into temperate U.S. Corn Belt maize germplasm sources to maintain the level of genetic diversity necessary for future advancement to take place. The utilization of exotic germplasm for specific traits, such as disease, pest, and stress resistance, and grain yield, is one of the main supporting factors for continuous genetic gains (Russell, 1986).

The extent to which exotic germplasm is used in temperate breeding programs is limited to how well the germplasm is adapted and the problems related to photoperiod sensitivity. Agronomic selection within breeding nurseries and crosses between exotic and adapted inbred lines or populations will help select potential exotic germplasm sources that can be utilized in temperate breeding programs. However, evaluation of exotic performance *per se* is virtually useless in the U.S. Corn Belt as a guide toward choosing materials for breeding use, mostly because of adverse photoperiod sensitivity (Goodman, 1985).

Consequently, the effect of photoperiod or daylength response is mostly a cosmetic problem, which can be eliminated even from descendents of 100% tropical crosses (Goodman, 1997). Procedures such as mass selection and the backcross technique have been used to remedy photoperiod problems. Once exotic material becomes adapted to temperate photoperiod day lengths, the material can be initiated into recurrent selection programs to help select for agronomic traits, such as grain yield.

Research into how adapted exotic maize populations combine with various elite domestic materials has increased over previous years. However, there is still a definite need to examine these types of population crosses to insure that genetic variability remains present



for helping broaden a narrowing germplasm base. This study used a Design II mating design to evaluate eight adapted Corn Belt populations and four exotic maize populations adapted to temperate environments by selection. The populations evaluated were categorized into two groups, Stiff-Stalk populations and Non-Stiff-Stalk populations, based on prior heterotic pattern classification and agronomic data from other studies. All parent populations used in the crosses, the population crosses themselves ( $F_1$ 's), and their reciprocal crosses, were evaluated under conditions of the central U.S. Corn Belt based on agronomic performance data. The objective of this study was to compare observed mid-parent heterosis estimates between crosses of Stiff-Stalk populations and Non-Stiff-Stalk populations. The second objective of this study is to determine if a maternal effect resides in maize with certain populations *per se* performing better as a male compared to their use as a female parent. Conclusions from this study may also allow for possible identification of new interracial heterotic patterns and provide an evaluation of previously determined heterotic patterns. The identification of possible heterotic patterns between adapted and tropical germplasm sources may allow future plant breeders the opportunity to have new germplasm resources for extraction of inbred line and the production of hybrids. Finally, conclusions regarding the occurrence of maternal or reciprocal effects in maize could be evaluated from this study.

## LITERATURE REVIEW

### Heterosis

**Identification of the Concept of Heterosis:** The phenomenon and manifestation of heterosis in maize, has resulted in the exploitation of maize as a major staple crop within the U.S. agricultural sector and the large-scale development of today's maize seed production and breeding programs. The concept of heterosis refers to the genetic expression of the superiority of a hybrid in relation to its parents in which a hybrid could be a cross between populations, or more commonly, between inbred lines (Miranda Filho, 1997). Duvick (1997) summarizes that heterosis in plants has been used on a large scale for the past 75 years through the use of carefully selected and reproduced hybrid cultivars.

Recognition of the occurrence of heterosis in crosses among maize open-pollinated cultivars was first identified by Darwin and Beal in the latter part of the late 18<sup>th</sup> and early 19<sup>th</sup> centuries. However, the use of variety crosses in exploiting heterosis never fully gained popularity since crossing among open-pollinated cultivars did not always result in a hybrid significantly better than the better parent, as suggested by Richey (1922). The potential of heterosis remained unutilized until Shull (1908, 1909, 1910) released his interpretations from his experiments with maize.

The beginning of the heterosis and the inbred-hybrid concepts were coined by George H. Shull (1908, 1909, 1910) based upon the conclusions drawn from the results of his inbreeding and crossing experiments. Shull (1908) described the genetic composition of an open-pollinated maize cultivar as a series of very complex hybrids produced by the combination of numerous elementary species. Shull (1909) stated that self-fertilization within the maize cultivar eliminated hybrid elements and reduced the strain to its elementary components by forming pure-lines that were homogenous and homozygous. Hallauer (1990) emphasized that when Shull intercrossed the pure-lines to develop single crosses, the agronomic performance of the cross was restored in relation to its inbred parents.

Hybrid vigor had resulted in crosses of the pure lines because heterozygosis (i.e., *heterosis*) would occur in crosses homozygous for different alleles (Hallauer, 1997a). At this time the beneficial effects of hybridization and the detrimental effects of inbreeding were well known prior to the 20<sup>th</sup> century (Zirkle, 1952). Shull, however, correctly interpreted

heterosis as the opposite of inbreeding depression and was the first to suggest how heterosis can be exploited in cultivar development (Bernardo, 2002). Based on the results of earlier studies, Shull (1909, 1910) correctly suggested the future course of plant breeding by: i) selfing within a heterogeneous population to obtain pure lines, ii) producing crosses between the pure lines, and iii) evaluating the crosses to determine the most productive cross.

**Gene Action Theory Responsible for Heterosis:** The rediscovery of Mendel's laws of inheritance in the early 1900's stimulated interest in forming an understanding of the genetic and biometrical basis of the occurrence of heterosis in maize. Because of the importance of maize and the heterosis manifested in maize crosses, breeders and geneticists have been active in studying the heterosis phenomenon and attempting to develop genetic models for its inheritance (Hallauer and Miranda, 1988). However, even today, the genetic mechanisms underlying heterosis are still largely unknown (Coors, 1997).

Although numerous hypotheses were suggested to explain the genetic basis of heterosis, two hypotheses have received the most attention: i) dominant favorable growth factors or dominance hypothesis, and ii) physiological stimulation or the overdominance hypothesis. Heterosis under the dominance hypothesis is produced by the masking of deleterious recessives in one strain by dominant or partially dominant alleles in the second strain. The dominance hypothesis was explicitly stated mathematically by Bruce (1910) based on Mendelian genetics in which heterosis would occur if the parents differed in gene frequency and dominance was present. The second hypothesis, the overdominance hypothesis, explained heterosis being due to heterozygote superiority and, therefore, increased vigor is proportional to the amount of heterozygosity. This non-Mendelian hypothesis, proposed independently by Shull and East in 1908, assumed there is a physiological stimulus to development that increases with the diversity of uniting gametes (Allard, 1960). In most situations, the dominance and the overdominance hypotheses lead to exactly the same expectations. Under the dominance hypothesis, decline in vigor is associated with increasing homozygosity; whereas with overdominance, decline in vigor is associated with decreasing homozygosity. The chief point of difference lies in the impossibility of obtaining homozygotes as vigorous as heterozygotes if single gene overdominance is important in heterosis (Allard, 1960).

Advocates to the overdominance hypothesis put forth two main objections toward the ideas suggested within the dominance hypothesis. First, if the dominance hypothesis is presumed correct, then inbred lines with the same agronomic performance as single cross hybrids should be obtained due to the accumulation by selection of all favorable dominant alleles. Second, if dominance were present, we would expect a skewed distribution from the expansion of the binomial  $(3 + 1)^n$  (Hallauer and Miranda, 1988). Reconciliation of these objections toward the dominance hypothesis was put to rest by Collins (1921) and Jones (1917). Jones (1917) suggested that many genes may affect yield and if linkage groups containing both dominant and recessive alleles were present, a series of precisely placed crossovers would be required to achieve an inbred with all dominant alleles. In favor of the dominance hypothesis, Jones (1917) argued that linkage between groups of favorable and unfavorable alleles would also lead to a theoretically symmetrical distribution. Collins (1921) disputed both objections emphasizing that if the number of loci controlling a trait was large (10 or more), finding a inbred line homozygous for all loci would be impossible. Collins also stated that skewness would be difficult to detect if the number of loci involved was large.

Crow (1948) believed dominance was an insufficient explanation to account for how heterosis occurred based on a mutation load argument. Crow stated that under the dominance hypothesis if all recessive mutations were removed from each locus in a random mating population, the maximum amount of increased performance (*i.e.*, heterosis) obtained by a hybrid compared with an equilibrium population would be 5% or less. The amount of heterosis manifested in the best hybrids usually exceeds 5%, allowing Crow to conclude that overdominance was the most likely explanation for heterosis.

Crow's (1948) overdominance viewpoint changed in favor of dominance later as Crow (1997) observed higher possible mutation rates in later experimentation in which selection and recombination occurred. The dominance hypothesis could now account for heterosis increases of 25% or more instead of being limited to increases of only 5%. These facts ruled Crow's earlier overdominance viewpoint as weak. Crow (1997) correctly summarized that occurrence of overdominance, or more precisely: *psuedo-overdominance*, in

earlier experimentation was a consequence of linkage disequilibrium or favorable dominants being linked to deleterious recessives.

Sprague and Miller (1950), Sprague and Russell (1956), and Penny *et al.* (1962) used recurrent selection to determine the type of gene action responsible for heterosis. In their independent studies, two heterozygous and heterogeneous populations of maize were each improved over several cycles of recurrent selection based on agronomic performance of crosses with inbred testers. Crosses were then made between the two populations to determine if overdominance was of primary importance; noting that the series A, A<sub>1</sub>, A<sub>2</sub>, *etc.*, B, B<sub>1</sub>, B<sub>2</sub>, *etc.* should exhibit an increasing degree of complementation to the tester parent as suggested by Sprague and Russell (1956). The two populations undergoing selection should become more alike genetically as selection progresses; however, the inter-crosses, A<sub>0</sub> x B<sub>0</sub>, A<sub>1</sub> x B<sub>1</sub>, A<sub>2</sub> x B<sub>2</sub> should exhibit a decreasing degree of heterozygosity and a decreasing yield trend if overdominance is of importance (Penny *et al.*, 1962). Both sets of results supported the dominance hypothesis because both populations *per se* and their respective crosses showed increased yields over successive cycles of selection. Simultaneously, the experiments indicated that the increase in heterosis was mainly due to additive and dominant gene effects within both the populations and the crosses.

A third hypothesis crediting epistatic effects has also been considered to explain the expression of heterosis in maize. Epistasis involves the interaction of alleles at two or more loci that could result in performance superior to that of independent loci (Fehr, 1991). Evidence of epistatic effects leading to heterosis among specific crosses of lines has occurred, but although unknown, these effects may be restricted to the specific cross *per se* and not attributed to the lines or populations used to produce the cross. However, despite occurrence of epistasis in maize, the dominance hypothesis is still the most widely accepted genetic hypothesis for the occurrence of heterosis.

**Heterosis Biometrical Requirements:** Advancement in quantitative genetic theory underlying the mechanisms required for the occurrence of heterosis rapidly progressed after presentation of the theories describing the genetic basis of heterosis. The conditions necessary to describe the quantitative genetic basis of heterosis are similar, but modernized,

to those presented by Bruce (1910) in his mathematical formulation of the dominance hypothesis.

Under a quantitative biometrical viewpoint, heterosis may occur whenever there is genetic divergence resulting in different gene frequencies between parents and some level of dominance (Miranda Filho, 1997; Falconer, 1960). If either or both of the conditions do not exist, heterosis will not be manifested (Hallauer and Miranda, 1988). If dominance exists controlling the trait, heterosis will be a function of the distribution of gene frequencies. Maximization of heterosis in crosses will occur when inbred lines are crossed in which the gene frequency of one allele is fixed ( $p=0$ ) in one line and the gene frequency of the other allele ( $p=1$ ) fixed in the other line. The same principle holds for crossing between populations, with only the difference that there is a distribution of gene frequencies in the range  $0 \leq p \leq 1$  (Miranda Filho, 1997).

Following the additive-dominance model, the mathematical expression of heterosis for each individual loci can be presented by the summation of the joint effects of all the loci in the following equation:

$$H_{F1} = \sum (p_i - r_i)^2 d_i ;$$

where:  $p_i$  is the frequency of the favorable allele at the  $i^{\text{th}}$  locus in one parent;  $r_i$  the frequency of the same allele in the other parent; and  $d_i$  is the deviation due to dominance (Miranda Filho, 1997). This equation represents the heterosis manifested between two inbred lines or populations resulting in  $F_1$  (first filial generation) progeny. The resultant heterosis produced in later filial generations is reduced by half for each successive generation of progeny developed. The reduction in heterosis occurs due to a decrease in additive and dominance effects upon continued random mating or selfing. Expression of heterosis in the  $F_2$  (second filial generation) is calculated as follows:

$$H_{F2} = \frac{1}{2} \sum (p_i - r_i)^2 d_i .$$

The notation of the variables used remains the same as the notation description of the equation for the expression of heterosis for  $F_1$  progeny.

Falconer and MacKay (1996) defined three conclusions that can be drawn from the above equations in explanation of the dominance and additive effects necessary for the occurrence of heterosis.

- 1) If some loci are dominant in one direction and some in the other, their effects will tend to cancel out regardless of dominance at individual loci.
- 2) The amount of heterosis will be something specific to each cross.
- 3) If the lines crossed are highly inbred, and so completely homozygous, the difference of gene frequency between them can only be 0 or 1.

The theory deriving the additive-dominance model equation:

$$H_{F_1} = \sum (p_i - r_i)^2 d_i ,$$

defining heterosis is used by researchers in studies to estimate mid-parent and high-parent heterosis. Mid-parent heterosis is defined as the difference in performance between the hybrid and the mean of the two parents (Falconer and MacKay, 1996) and is the more commonly used model for estimating heterosis. Likewise, high-parent heterosis is a comparison of the performance of the hybrid with that of the best parent in the cross (Fehr, 1991). Derivation of mid-parent heterosis and high-parent heterosis mathematically is achieved through the use of Equation 1 for mid-parent heterosis and Equation 2 for high-parent heterosis:

$$\text{Equation 1) } H_{mp} = \overline{F_1} - \overline{MP}$$

$$\text{Equation 2) } H_{hp} = \overline{F_1} - \overline{HP}$$

where,  $\overline{F_1}$  is the mean of the hybrid cross between parents,  $\overline{MP}$  is the average mean performance of the two parents or the mid-parent value, and  $\overline{HP}$  is the mean agronomic performance of the highest parent used in the cross or the high-parent value. Mid-parent and high-parent heterosis can also be calculated as a percentage by dividing the difference between the  $F_1$  hybrid and the mid-parent or high-parent mean by the mid-parent or high-parent value and multiplying the value by 100. To differentiate between the two types of mid-parent and high-parent heterosis calculated in this study, the aforementioned two heterosis values will be termed percent mid-parent heterosis and percent high-parent heterosis, respectively. Calculation of percent mid-parent heterosis

and percent high-parent heterosis mathematically is achieved through the use of Equation 3 for percent mid-parent heterosis and Equation 4 for percent high-parent heterosis:

$$\text{Equation 3) } H_{mp} = \frac{\overline{F_1} - \overline{MP}}{\overline{MP}} * 100$$

$$\text{Equation 4) } H_{hp} = \frac{\overline{F_1} - \overline{HP}}{\overline{HP}} * 100$$

where;  $\overline{F_1}$  is the mean of the hybrid cross between parents,  $\overline{MP}$  is the average mean performance of the two parents or the mid-parent mean, and  $\overline{HP}$  is the mean agronomic performance of the highest parent used in the cross or the high-parent mean. These two heterosis calculations are expressed as percentages, but percentages are difficult to interpret from a quantitative genetic point of view, and statistical tests of percentage mid-parent heterosis and percentage high-parent heterosis are nearly impossible (Lamkey and Edwards, 1997). However, statistical tests of significance on heterosis estimates can occur on the mid-parent and high-parent heterosis values when expressed as just the difference between the  $F_1$  population cross hybrid and the mid-parent or high-parent values.

### **Heterotic Groups and Their Patterns**

**Usage of Heterotic Groups and Patterns:** Use of heterotic patterns greatly enhances the overall success of hybrid breeding programs. Knowledge of heterotic patterns established among cultivars has had important implications for selecting inbred lines as potential seed stock (Hallauer and Miranda, 1988). Therefore, heterotic groups are used to classify groups of germplasm that will have maximum expression of heterosis in crosses of inbred lines from distinct groups (Hallauer, 1997b). Hybrid cultivars are then subsequently made by crossing inbreds derived from source populations classified in two complementary heterotic groups, which together comprise a heterotic pattern (Bernardo, 2002).

Evolution of heterotic groups and patterns did not begin with the development of the many races, accessions, and cultivars present in maize. Instead, heterotic groups have evolved over time and space with initial beginnings stemming from the increased use of the inbred-hybrid theory for the development of single crosses and double crosses in the 1920's. At this time, evidence detailing the expression of heterosis had been demonstrated between two single crosses crossed together to form double crosses. However, limited attention had been given to the origin of the inbred lines deriving the makeup of the early double crosses.



Performance of the lines in crosses suggested those certain combinations of germplasm deriving the crosses were better than others; determining how different germplasm sources could be used successfully in crosses. Results reported by Eckhart and Bryan (1940) suggested that greater productivity in double crosses occurred when genetically similar inbred lines were used to produce the parental single crosses. Double cross hybrids are then produced by hybridization of two parental single crosses from opposing germplasm sources genetically diverse by origin. This principle allowed later plant breeding researchers to believe that ‘the manifestation of heterosis usually depends on the genetic divergence of the two parental varieties’ (Hallauer and Miranda, 1988).

**Heterotic Group Identification:** Identification of heterotic groups and patterns based on the principle of genetic divergence was discussed by Tsotsis (1972). Tsotsis’s goal was to determine heterotic response among a group of open-pollinated cultivars. Assignment of the cultivars to two broad-based populations was determined based on the performance of each cultivar in crosses. The logical sequence was then to cross and test populations or inbred lines between the two gene pools (Hallauer and Miranda, 1988).

Germplasm sources changed from open-pollinated cultivars to pedigree selection within  $F_2$  populations of elite lines crosses for extraction of inbred lines after the initial sampling of open-pollinated cultivars. However, the identification of possible heterotic groups was not defined until yield performance testing data of inbred lines in crosses was established. Melchinger and Gumber (1998) highlighted the following criteria to follow when identifying heterotic groups and patterns for use in breeding programs:

- 1) high mean performance and large genetic variance in the hybrid population;
- 2) high *per se* performance and good adaptation of the parent populations to the target region(s); and
- 3) low inbreeding depression, if hybrids are produced from inbreds.

When a smaller number of populations with known origin are used it is common practice to evaluate diallel or factorial crosses among them (Melchinger, 1997). However, if a larger number of germplasm sources are available and established heterotic groups or proven testers exist, the performance of testcrosses between them are usually taken as the main criteria for choice and grouping of materials (Melchinger, 1997). Overall, agronomic

performance based upon combining ability among and between population and inbred line crosses determined potential heterotic groupings and patterns.

Germplasm evaluation based upon combining ability allowed plant breeders an effective way of classifying maize populations relative to overall cross performance. Populations exhibiting high combining ability are then considered for inbred line development and improvement through methods of recurrent selection. During the development of the quantitative genetic theory of heterosis, the concept of combining ability was refined by Sprague and Tatum (1942) to partition the term into the expressions of general combining ability (GCA) and specific combining ability (SCA). They defined GCA as the average performance of a line or population in hybrid combination when expressed as a deviation from the mean of all crosses, attributed primarily to additive gene effects. SCA, based on non-additive gene effects, described instances in which certain hybrid combinations are either better or poorer than would be expected based on the average performance of the parents included. Estimation of GCA and SCA values have been used extensively in maize population improvement programs as recurrent selection methods were designed to provide systematic, incremental genetic improvements in genetically broad-based populations for complex traits (Hallauer, 1997a).

Development of different recurrent selection methods was based on the types of genetic effects considered important in the expression of quantitative traits: recurrent selection for GCA if additive genetic effects are of greater importance along with recurrent selection methods for SCA if non-additive genetic effects are of greater interest (Hallauer, 1994a). Comstock *et al.* (1949) suggested reciprocal recurrent selection to maximize selection for both general and specific combining ability when both additive and non-additive effects are of importance. For breeding programs emphasizing the development of inbred lines and hybrids from populations derived from distinct heterotic groups, it seems reciprocal recurrent selection methods should be used to enhance the heterotic pattern (Hallauer, 1997a).

Conceptualization of combining ability has resulted with heterotic groups and their patterns, becoming established within most of the world's major maize production areas. In the U.S. Corn Belt, maize breeders have utilized and emphasized selection within the

Lancaster Sure Crop x Reid Yellow Dent or Iowa Stiff Stalk Synthetic (Stiff-Stalk) x Lancaster Sure Crop (Non-Stiff-Stalk) heterotic patterns for nearly 50 years (Baker, 1984; Sprague, 1984; Hallauer, 1997c). The extensive use of germplasm within the Stiff-Stalk x Non-Stiff-Stalk heterotic pattern resulted from the germplasm's wide distribution and availability to plant breeders for hybridization studies, along with the extensive amount of yield trial data available for evaluation of the germplasm.

Further agronomic evaluation of heterotic patterns, such as the well-known Stiff-Stalk x Non-Stiff-Stalk heterotic pattern, has been conducted to evaluate heterotic patterns and the heterotic groups making up the heterotic patterns to determine if potential maternal or reciprocal effects exist among different population germplasm pools or in the population crosses. Maternal effects occur when the phenotype or environment of a mother plant affects the phenotype of her offspring via some mechanism other than the transmission of genes (Fox, 2000). Maternal effects typically are present only in the first generation of progeny. Maternal effects can also dictate how the population is used as a parent in crosses, while the corresponding reciprocal effect occurs due to how the heterotic pattern is used in making the cross. A reciprocal effect would result if a normal cross using a Stiff-Stalk female with a Non-Stiff-Stalk male heterotic pattern was significantly different in agronomic performance (*i.e.*, phenotypic characteristics) when compared with the reciprocal cross where a Non-Stiff-Stalk female is crossed with a Stiff-Stalk male. In early studies, maternal effects and reciprocal effects in heterotic groups and heterotic patterns were studied through examination of reciprocal crosses in which agronomic performance of the reciprocal cross is evaluated against the normal version of the cross. But in 1952, Comstock and Robinson (1952) stated that nongenetic maternal effects usually are assumed absent in the estimation of components of genetic variances within a maize population. Therefore, since maternal and reciprocal effects are assumed to be absent or small in maize, reciprocal crosses usually are not grown (Hallauer and Martinson, 1975).

Today, recognition of the absence of maternal and reciprocal effects in maize has prevented many studies from being done in plant breeding in which population cross and population cross performance *per se* is evaluated for these effects based on agronomic performance data. Plant researchers instead have applied more attention into studying the

emphasis of maternal and reciprocal effects in different maize cytoplasm pools, with most research interested in examining these effects and associated *xenia* (cross-pollination) effects in cytoplasmic male-sterile germplasms (*i.e.*, Texas male sterile cytoplasm). One such study was conducted by Hallauer and Martinson (1975) who produced and evaluated crosses and reciprocal crosses among nine inbred lines of maize in normal *rfrf* (Nrf) and Texas male sterile *RfRf* (TRf) cytoplasms. The objective of the analysis was to determine if maternal and reciprocal effects for yield and other agronomic traits existed in 72 normal cytoplasm single crosses and 72 Texas male sterile cytoplasm crosses after inoculation with the fungus *Bipolaris maydis* (Nisikado) Shoemaker, race T. Hallauer and Martinson (1975) concluded that although not large, significant maternal mean squares were detected for all traits except stand among both cytoplasms. The analysis also reported significant reciprocal effects for the trait stalk lodging in both cytoplasms, but no reciprocal effects were found significant for the agronomic trait grain yield.

The importance of maternal and reciprocal effects for the agronomic trait cold tolerance was studied by Cowen (1985) evaluating the BS13(SCT)C5 population (a normal cytoplasm population) in a Design II mating design. Reciprocal crosses also were produced. The Design II analysis successfully showed maternal effects existing for the two cold tolerance traits, percent emergence at 200 growing degree days, and seedling vigor at 400 growing degree days. All reciprocal effects for cold tolerance traits were nonsignificant in the combined analysis.

The possibility of significant maternal effects occurring for grain yield and other agronomic traits can be based on phenotypic characteristics in the different heterotic groups selected for through the use of recurrent selection and pedigree selection programs. Troyer (2000) stated that selection within the Stiff-Stalk heterotic group has characterized the heterotic group with plants that have smaller but more erect tassels, medium-length, large diameter ears with smaller kernels, and with more kernel rows present on the ear. These traits allow Stiff-Stalk germplasm to be used more effectively as the female parent in crosses. However, germplasm within the Non-Stiff-Stalk heterotic group, as stated by Troyer (2000), was selected for and characterized as plants that have larger and erect tassels, smaller diameter and lengthy ears, larger kernels, and with fewer kernel rows present on the ear.

Phenotypic traits such as these have allowed Non-Stiff-Stalk germplasm to serve more effectively as the male parent in most crosses. The heterotic pattern combination of a female Stiff-Stalk parent and a male Non-Stiff-Stalk parent has allowed production of high-yielding hybrids, whereas the reciprocal cross generally has produced hybrids showing a decline in heterosis.

Despite the large amount of interest presented for the heterotic groups within the heterotic pattern Reid Yellow Dent by Lancaster Sure Crop (Stiff-Stalk by Non-Stiff-Stalk); both heterotic groups having good combining abilities and the potential of exhibiting maternal effects. Some researchers showed concern that a large number of germplasm collections had not yet been evaluated for agronomic performance based on yield trial information. Kauffmann *et al.* (1982) evaluated yield and mid-parent heterosis among crosses of open-pollinated cultivars to identify possible heterotic patterns. Populations included in the study were Reid Yellow Dent, Leaming, Midland, Lancaster Sure Crop, and Hays Golden. Kauffmann *et al.* (1982) reported that the Leaming and Midland cultivars were a potentially useful heterotic pattern for the U.S. Corn Belt area.

Following similar experimental studies, potential heterotic patterns have been suggested for the tropical areas. In Mexico, crosses that include lines from ETO composite and Tuxpeño are an important heterotic pattern, but the wealth of germplasm available in Mexico would not preclude other important heterotic patterns (Hallauer *et al.*, 1988). Testcross studies conducted by Beck *et al.* (1990) concluded that CIMMYT populations 23 and CIMMYT pool 20 should be considered as a heterotic pattern for early maturity areas. Ten tropical heterotic patterns identified and exploited by breeders in tropical areas were listed by Goodman (1985) based upon testcross performance. Makeup of the ten heterotic patterns included only eight races, but emphasis was directed to the following five: Tuxpeño, Cuban Flint, Tuson, Coastal Tropical Flint, and Chandelle. Also, the Tuxpeño race in combination with Suwan-1 has recently been suggested by Crossa *et al.* (1990) for consideration as a potential heterotic pattern for tropical areas.

Despite the numerous heterotic patterns available within each major maize production area, there is very little current information available determining heterotic patterns between various elite, exotic germplasms and various elite domestic materials (Goodman, 1985;

Gerrish, 1983). Deterrents, such as adverse photoperiod response, adaptation problems, and linkage effects, have limited the extent to which progress has been made in development of exotic by temperate heterotic patterns. However, plant breeding methodologies such as the backcross technique (Gerrish, 1983) and mass selection (Hallauer, 1994b) have been used successfully to adapt exotic populations to temperate conditions. With exotic populations now adapted to U.S. Corn Belt temperate conditions, the identification of exotic by temperate heterotic patterns begins.

Testcross evaluation allowed Goodman (1985) to suggest Tuson by U.S. Southern Dents as a potentially useful heterotic pattern for the Southern U.S. Corn Belt area. Based on diallel crosses of seven U.S. Corn Belt cultivars and Mexican Dent (derived from Tuxpeño and Celeya), Potchefstroom Pearl, and ETO composite cultivars, Mungoma and Pollak (1988) concluded that BSSS(R)C10 (Reid Yellow Dent germplasm) and Mexican Dent should be evaluated as a potential heterotic pattern. Their results showed BSSS(R)C10 and Mexican Dent having the highest yield response allowing consideration of the cross in U.S. inbred-hybrid breeding programs. Michelini and Hallauer (1993) reported potential heterotic patterns, based on the observance of high levels of mid-parent heterosis, when either Tuxpeño or Suwan-1 was crossed with BS13, a strain of Iowa Stiff Stalk Synthetic, and when Suwan-1 was crossed with BS26, a strain of Lancaster Sure Crop germplasm.

Evaluation of four U.S. Corn Belt cultivars and four adapted exotic cultivars in diallel crosses provided Echandi and Hallauer (1996) with results suggesting BSSS(R)C12 (Reid Yellow Dent) x BS29 (Suwan-1) should be used in hybrid combinations. Echandi and Hallauer (1996) reported BS29 had significantly greater yield in crosses with Iowa Stiff Stalk Synthetic germplasm (BSSS) suggesting BS29 be included in the Lancaster Sure Crop heterotic group. They stated BS16(I) (ETO composite), BS27 (Antiqua), and BS28 (Tuxpeño) had similar cross performance with U.S. Corn Belt cultivars, but no clear indication was evident to decipher which heterotic group (Reid Yellow Dent or Lancaster Sure Crop) they belonged to.

## **Exotic Germplasm**

**Increasing Genetic Diversity with Exotic Germplasm:** The introduction of exotic germplasm into temperate breeding programs was suggested by Brown (1953) and Wellhausen (1965) for increasing the level of genetic diversity among temperate U.S. Corn Belt populations. Exotic germplasm generally is considered to include all sources of unadapted germplasm: domestic, temperate, and tropical (Goodman, 1985). Current discussion over lack of genetic diversity among maize germplasm sources should be irrelevant since germplasm sources for maize are extensive. There are 25,000 to 30,000 accessions in gene banks representing different cultivars and strains of the 130 or more races of maize (Hallauer, 1997a). However, according to Brown (1975), U.S. maize breeding programs have devoted their efforts toward breeding in only two or three of the existing American races.

Genetic diversity within different germplasm sources represents the foundation breeding material necessary to any maize breeding program. If genetic diversity is not present in the breeder's populations, selection will be neither effective nor possible (Hallauer and Sears, 1972). Wellhausen (1965) proposed that use of exotic germplasm sources would greatly increase the potential improvement of maize germplasm and enhance heterosis due to increased genetic diversity. Increased genetic diversity arises due to exotic germplasm providing new combinations of novel alleles upon hybridization with adapted germplasm that were either not present before or present in the wrong allelic form (*i.e.*, dominant vs. recessive). Albrecht and Dudley (1987) emphasized that the use of exotic germplasm provides a source of genes for specific traits, such as disease, pest, and stress resistance and a source of favorable alleles for yield to increase genetic variation and enhance heterosis. In most instances exotic germplasm has traditionally been used in the United States as a last resource of disease and insect resistance (Goodman, 1997).

Despite exotic germplasms' advantages, the general trend toward use of exotic germplasm seems to be static according to Duvick (1981, 1984), although there has been a gradual increase of exotic germplasm into the genetic germplasm base of maize in the United

States over the past decade. Goodman (1985) listed several reasons regarding the limited use of exotic germplasm:

- 1) Adverse photoperiod response masks desirable characters;
- 2) Improvement of landrace materials is 40 years behind currently used breeding materials;
- 3) Linkages between favorable and unfavorable genes in exotic by adapted populations cannot be readily broken; and
- 4) There is no adequate basis for choosing the best exotics for use in plant breeding.

Adaptation problems due to photoperiod and temperature effects have restricted the potential use of tropical exotic maize germplasm into temperate maize breeding areas. Goodman (1997) stated that photoperiod effects, or day length response, is mostly a cosmetic problem, which can be diminished or eliminated by selection. Hallauer and Sears (1972) compared two procedures for integrating ETO composite into a central U.S. maize breeding program: i) mass selection for earlier silking and ii) crossing ETO composite with six early inbred lines. Their results suggested that mass selection was effective for adapting a 100% exotic maize population to U.S. Corn Belt breeding programs. Also, crossing exotic germplasm with adapted germplasm and then intermating worked successfully to produce a 50% exotic germplasm called BS2. BS2 responded similarly to the commonly used high-yielding Iowa Stiff Stalk Synthetic (BSSS) population.

The mass selection procedure continues to be used today as an excellent procedure to adapt exotic germplasm to temperate maize breeding areas. Three studies support the potential of mass selection. According to Troyer and Brown (1972), mass selection has proven effective for adaptability. The Antiqua composite population was adapted to U.S. Corn Belt temperate areas following six cycles of mass selection for early silk emergence. San Vicente and Hallauer (1993) reported mass selection within the Antiqua composite allowed for a 17-day earlier flowering date compared with the original population. Simultaneously, mass selection increased the agronomic performance of the Antiqua composite in grain yield and other traits to a level similar to elite adapted cultivars. Improvement in two exotic maize populations, Tuxpeño (BS28) and Suwan-1 (BS29), by mass selection was reported by Hallauer (1994b). Hallauer's results suggested that after five



cycles of mass selection, the Suwan-1 and Tuxpeño populations had silking dates 12-days and 16-days earlier compared with the original unadapted populations. Grain yield also was increased within the Suwan-1 population by 6.0 q/ha and in the Tuxpeño population by 15 q/ha following selection.

**Exotic Germplasm Introgression Procedures:** The procedures necessary to introgress exotic germplasm into adapted temperate maize and the amount of exotic germplasm to introgress has been explored by numerous researchers (Mungoma and Pollak, 1988; Crossa and Gardner, 1987; Michelini and Hallauer, 1993; Moll *et al.*, 1962). Before introgression of exotic germplasm into adapted germplasm begins, the choice of germplasm to include has to be considered. In the past, limited yield trial information existed on the evaluation of exotic by adapted materials and since exotic germplasm performance *per se* is a poor indicator of agronomic performance, the breeder must use his own experiences in selection of the proper exotic germplasm materials. Salhuana *et al.* (1994) reported that the Latin American Maize Project (L.A.M.P.) has eliminated many of the problems associated with initial evaluation of germplasm-accession sampling. Also, the Germplasm Enhancement of Maize (G.E.M.) project, which is a follow-up project to L.A.M.P., is a multi-institutional, public-private, cooperate endeavor used to quickly inject elite exotic germplasm into public and private breeding programs (Salhauna *et. al.*, 1994). According to Goodman (1997), G.E.M. uses elite germplasm accessions that are crossed to elite domestic private lines forming new populations for inbred line extraction.

Patience by the breeder must be utilized before the initiation of selfing in recently hybridized exotic by adapted cultivars, as disaster will strike since inbreeding depression is severe and few vigorous inbred lines will be obtained (Hallauer and Miranda, 1988). Eventually, the germplasm material developed from selfing will be discarded and the plant breeders labor, effort, and time foregone as an expense to this mishap. Two cycles of recombination, following the initial random mating cycle, of the best selected exotic by adapted progenies before selfing limits the severity of inbreeding depression that would occur. The practice of recombination and random mating are also important in newly developed adapted by exotic populations to limit linkage effects (Lonnquist, 1974).

Continued improvement in adapted exotic germplasm populations can be enhanced by the use of recurrent selection to help increase allelic frequencies within the population for agronomic trait selection, such as yield, important within the U.S. Corn Belt area. Recurrent selection is broadly defined as the systematic selection of desirable individuals from a population followed by recombination of the selected individuals to form a new population (Fehr, 1991). All populations used in this study have been improved in agronomic performance through the use of recurrent selection. If recurrent selection is successful, the population improved will be superior to the original population in both mean performance and to the performance of the best individuals within the population without losing genetic variability. Iglesias and Hallauer (1990) used  $S_2$  recurrent selection in three populations including exotic germplasm. The populations used, along with the corresponding proportion of exotic germplasm present within each, are listed as follows: BS16 – 100% exotic, BS2 – 50% exotic, and BSTL – 25% exotic. Several cycles of recurrent selection were preformed for each population and Iglesias and Hallauer (1990) results showed significant increases in grain yield for intermediate cycles of selection at average rates of 3.4, 3.8, and 4.2 q/ha. However, the three populations in later cycles had limited response to improvement in grain yield possibly due to either rapid fixation of important alleles or genetic drift after selection occurred.

In most instances, the observance of heterosis toward agronomic performance occurred when exotic germplasm was introgressed into crosses with adapted germplasm. In studies derived from crossing exotic germplasm sources of different ancestral relationships and levels of geographical separation to adapted temperate maize germplasm, Moll *et al.* (1962) and Moll *et al.* (1965) concluded that heterosis increased in genetically divergent crosses, while extremely divergent crosses resulted in a decrease in heterosis. Kramer and Ulstrup (1959) screened 1066 exotic maize introductions for agronomic performance traits and sources of resistance to forms of rust associated with the U.S. Corn Belt area. Their results suggested that screening exotic germplasm for specific characters, such as for disease resistance, is beneficial and rewarding; unfortunately, selecting germplasm for increased yield potential proved less rewarding.

Efron and Everett (1969) studied the potential role of exotic germplasm in improving maize hybrids for short season temperate zones by examining two components: i) dry matter in stover and ii) dry matter in grain. Their results concluded that for stover dry matter, exotic germplasm appeared to be an excellent material for improving present hybrids; for grain production the materials were not so promising. Efron and Everett (1969) suggested that a recurrent selection plan focusing on the concentration of desirable gametes from selected individuals is necessary, since mere crossing of introduced germplasm does not lead to automatic improvement.

The amount of exotic germplasm to introgress into adapted U.S. Corn Belt germplasm has been considered and researched. Crossa *et al.* (1987) found that populations consisting of 25% exotic germplasm did not yield significantly different from those containing all adapted exotic germplasm, but yielded better than populations containing 50% exotic germplasm. Examination of 90 S<sub>1</sub> families developed from three populations with different levels of exotic germplasm introgressed into an adapted population was studied by Crossa and Gardner (1987). Michelini and Hallauer (1993) examined crosses of seven exotic populations developed with various proportions of exotic germplasm and two U.S. Corn Belt populations to determine the proportion of exotic germplasm necessary to exemplify superior agronomic performance. In evaluation of the crosses, Michelini and Hallauer (1993) concluded that higher grain yields were obtained for the crosses of adapted by exotic germplasm containing 50% exotic germplasm.

The potential of introgression of exotic germplasm into adapted populations as a method to increase the genetic diversity through the addition of more favorable alleles into existing germplasm sources has been recognized. Research in plant breeding has recognized the potential of adapted exotic populations such as Tuxpeño, Suwan-1, Midland, Leaming, and others used in crosses with adapted germplasm, to increase the overall agronomic performance of today's maize cultivars. Studies have shown that selection programs and population improvement programs used simultaneously can help improve and adapt exotic populations to U.S. temperate breeding areas. However, Hallauer and Miranda (1988) emphasized that the breeder must have time and patience with the use of exotic germplasm as immediate payoffs should not be expected, but long-range payoffs seem likely.

## Design II Mating Design

**Principles of the Design II Mating Design:** Population crosses developed in this study were modeled after the mechanics of the Design II (DII) mating design. Developed in North Carolina by Comstock and Robinson (1948, 1952), the DII mating design is described as a factorial design in which different sets of males and females are used as parents for cross development. This design is unlike the more commonly used diallel mating design that utilizes the same parents as both females and males in crosses and is illustrated in Figure 1. Although the Design II mating design has not been used nearly as extensively in maize as the diallel, the Design II mating design seems to merit further consideration (Hallauer and Miranda, 1988).

The DII is a mating design that is appropriate for most crop species and in some respects cross development can be easier for self-fertilizing species than for cross-fertilizing species (Hallauer, 2002). Since different sets of parents are included as males and females, a greater number of parents can be evaluated with fewer cross permutations being made. Therefore, for a fixed number of experimental units, approximately twice as many parents

Diallel					Design II				
Parents (females)	Parents (males)				Parents (females)	Parents (males)			
	1	2	3	4		1	2	3	4
1	---	X <sub>12</sub>	X <sub>13</sub>	X <sub>14</sub>	5	X <sub>51</sub>	X <sub>52</sub>	X <sub>53</sub>	X <sub>54</sub>
2	X <sub>21</sub>	---	X <sub>23</sub>	X <sub>24</sub>	6	X <sub>61</sub>	X <sub>62</sub>	X <sub>63</sub>	X <sub>64</sub>
3	X <sub>31</sub>	X <sub>32</sub>	---	X <sub>34</sub>	7	X <sub>71</sub>	X <sub>72</sub>	X <sub>73</sub>	X <sub>74</sub>
4	X <sub>41</sub>	X <sub>42</sub>	X <sub>43</sub>	---	8	X <sub>81</sub>	X <sub>82</sub>	X <sub>83</sub>	X <sub>84</sub>

Figure 1. Comparison of the diallel and design II mating designs for the possible crosses among parents (adapted from Hallauer and Miranda, 1988).

can be used in the experiment (Hallauer and Miranda, 1988). Similarly, because the DII is a cross-classification scheme, the DII interprets sources of variation for males, females, and the interaction of males and females used within the study (Comstock and Robinson, 1948, 1952; Cockerham, 1963; Garretsen and Kuels, 1978; Hallauer and Miranda, 1988).

**Analysis of the Design II Mating Design:** These effects of variation are portrayed in the following mathematical model of the DII:

$$\text{Model } Y_{ijk} = \mu + m_i + f_j + (mf)_{ij} + e_{ijk},$$

where

$Y_{ijk}$  = the  $k^{\text{th}}$  progeny of male parent  $i$  mated to female parent  $j$ ,  $j \neq i$ ;

$\mu$  = the overall mean;

$m_i$  = the effect of the  $i^{\text{th}}$  male;

$f_j$  = the effect of the  $j^{\text{th}}$  female;

$mf_{ij}$  = is the interaction effect between the  $i^{\text{th}}$  male and the  $j^{\text{th}}$  female; and

$e_{ijk}$  = the error effect associated with  $ijk^{\text{th}}$  observation.

Comstock and Robinson (1948, 1952) explained several different methods to analyze the DII based on whether the parents used in the experiment are a fixed set of populations or lines (Model I) or a random sample of lines or populations describing a reference population (Model II). Based on a fixed group of parents, the Model I provides two independent estimates of GCA effects for males and females and SCA effects for male x female interaction. Appropriate F-tests can be made to test for the differences among males and among females and for the interaction of males and females (Hallauer and Miranda, 1988). Likewise, the Model II analysis provides valid estimates of genetic components of variance, which characterize the population from which the parents were randomly obtained. Several criteria need to be considered to develop valid and unbiased genetic components of variance estimates.

The necessary criteria for valid variance estimates for the Model II analysis were listed and described by Comstock and Robinson (1948, 1952) as followed:

- a) random choice of individuals mated for production of experimental progenies;
- b) random distribution of genotypes relative to variation in the environment;
- c) no nongenetic maternal effects;
- d) regular diploid behavior of meiosis; and
- e) no correlation of genotypes at separate loci, *i.e.*, no linkage or linkage disequilibrium among genes.

Ultimately, the Model II analysis provides the researcher with two precise and unique estimates of  $\sigma_A^2$  (one estimate for males; one estimate for females), along with a precise estimate of  $\sigma_D^2$  being estimated from the mean squares errors.

Examination of the assumption of no nongenetic maternal effects will be determined experimentally in this DII study with the inclusion of reciprocal crosses. In most DII studies, emphasis has been placed on cross development and variance component analysis alone, leaving reciprocal cross development to measure maternal effects not being considered. Research findings suggest only several DII studies including reciprocal crosses have been conducted, neither of which dealt with heterotic pattern identification. One example of a DII with reciprocals was conducted with *Drosophila* (Cockerham and Weir, 1977), the other was determination of cold tolerance in maize (Cowen, 1985). In Cowen's DII study, which followed the mechanics of a Design II model II, she estimated maternal effects as half the difference in the average performance of a line when used as a female and as a male. Reciprocal effects were estimated as the deviation of the mean for a specific cross from the predicted value based on male, female, male x female interaction and maternal effects (Cowen, 1985). Cowen concluded that when the cross performance of a line used as a female was compared to its use as a male, the line performed better as a male. Significant maternal effects for cold tolerance were also reported in the study. Consequently, the evaluation and analysis of reciprocal effects in both DII studies was not as simple or straightforward of an approach as previously anticipated.

## MATERIALS AND METHODS

### Genetic Materials

Eight U.S. Corn Belt and four adapted exotic maize populations were used in this study. Heterotic relationships are well known within both U.S. Corn Belt and adapted exotic maize populations, whereas limited information is available for heterotic pattern relationships between them. All populations have been improved over several cycles of recurrent selection. Information on each population is presented.

1. BSSS(R)C14 – A strain developed from the Iowa Stiff Stalk Synthetic (BSSS) population after being improved through 14 cycles of reciprocal recurrent selection. BSSS was synthesized in the 1930's by intercrossing 16 inbred lines selected for good stalk quality and the lines were primarily of Reid Yellow Dent origin (Sprague, 1946).

2. BSCB1(R)C14 – A strain developed after 14 cycles of reciprocal recurrent selection improvement in the Iowa Corn Borer Synthetic (BSCB1) population. BSCB1 was synthesized in the 1940's from 12 inbred lines with acceptable levels of resistance to the first generation European corn borer (*Ostrinia nubilalis* Hübner) (Hallauer *et al.*, 1974).

3. BS10(FR)C14 – A strain developed after 14 cycles of full-sib reciprocal recurrent selection improvement in the Iowa Two-Ear Synthetic (BS10) population. BS10 was developed by intermating 10 inbred lines with a prolific tendency and the lines were primarily of Reid Yellow Dent germplasm (Russell *et al.*, 1971).

4. BS11(FR)C14 – A strain developed after 14 cycles of full-sib reciprocal recurrent selection improvement of the Pioneer Two-Ear Synthetic #1(PHPRC) population. BS11 was developed by W.L. Brown of Pioneer Hi-Bred International, Inc. and BS11 was formed by crossing southern prolific material, Caribbean material and U.S. Corn Belt Lines (Hallauer, 1967).

5. BSK(S)C11 – A strain of Krug High I Syn. 3 (BSK) that was improved by 11 cycles of  $S_1$  and  $S_2$  intrapopulation recurrent selection. The base population – BSK, a strain of the open pollinated variety “Krug Yellow Dent”, was developed at the Nebraska Agricultural Experimental station and designated “Krug High I Syn. 3” (Lonnquist, 1949). Krug High I Syn. 3 was random mated in Iowa and coded BSK (Tanner, 1984).

6. BSK(HI)C11 – A strain of Krug High I Syn. 3 (BSK) that was improved through 11 cycles of half-sib recurrent selection (Tanner, 1984). Lines and crosses used as testers in the development of the BSK(HI)C11 strain have been the double cross IA 4659 ((WF9 X W22) X (B14 X M14)), the parental single crosses of IA4659, 'Krug 755', as well as B73.

7. BS13(S)C9 – A strain developed from the Iowa Stiff Stalk Synthetic (BSSS) population by seven cycles of half-sib selection and nine cycles of  $S_2$  selection. BS13 is a breeding population that should be useful for extraction of lines that have high yield as lines *per se* and good combining ability with lines of 'Lancaster Sure Crop' background (Hallauer and Smith, 1979).

8. BS16(S)C2 – A strain of 'ETO Composite' that has been improved through two cycles of  $S_1$  recurrent selection. BS16 was developed from the original 'ETO Composite' population through six cycles of mass selection for climate adaptability. (Hallauer and Smith, 1979). All BS16 strains include 100% tropical germplasm and are adapted to central U.S. Corn Belt environments (Echandi and Hallauer, 1996).

9. BS26(S)C4 – A strain that has had four cycles of  $S_1$  recurrent selection. The development of BS26 was initiated in 1977 by crossing 15 inbred lines (primarily C103 germplasm) with BSL(HI)C5, BSL(S)C6, and BSTL(S)C2 (Hallauer, 1986). Germplasm contained in the BS26 population is mostly of Lancaster Sure Crop origin.

10. BS28(R)C3 – A strain developed from the improvement of the BS28 population (Tuxpeño germplasm) after three cycles of reciprocal recurrent selection with BS29 as the tester. Population BS28 was developed from a composite of primarily Tuxpeño germplasm (Hallauer, 1994b). The BS28 population was adapted for the central U.S. Corn Belt area after five cycles of mass selection for earlier flowering.

11. BS29(R)C3 – A strain developed from three cycles of reciprocal recurrent selection improvement in the BS29 population with BS28 as the tester. Population BS29 was developed from Suwan-1(S)C6 (primarily Caribbean germplasm), which was developed in Thailand (Hallauer, 1994b). Adaptation of BS29 to central U.S. Corn Belt environments was achieved after five cycles of mass selection for earlier flowering.

12. BS34(S)C4 – A strain developed after four cycles of  $S_1$  and  $S_2$  recurrent selection within the BS34 population. BS34, commonly called Midland Yellow Dent,



originated and is adapted to southeastern Kansas. Midland Yellow Dent's phenotypic expression in Iowa resembles tropical germplasm since it is vigorous, leafy, and has heavy stalks (Carena, 1994).

### **Field Techniques**

Design II population crosses included in this study were produced at the Iowa State University Agronomy Research Farm in Ames, Iowa, during the 2001 summer. One requirement of the Design II was that different sets of males and females be used to make the crosses. Therefore, the 12 populations were categorized according to previous heterotic pattern classifications based on fitting into either one of two groups: 1) the Stiff-Stalk Synthetic group or 2) the non-Stiff-Stalk Synthetic group. The seven populations classified in the Stiff-Stalk Synthetic group were: BS10(FR)C14, BS13(S)C9, BS28(R)C3, BS34(S)C4, BSK(HI)C11, BSK(S)C11, and BSSS(R)C14. The remaining five populations classified in the Non-Stiff-Stalk Synthetic group were: BS11(FR)C14, BS26(S)C9, BS29(R)C3, BS16(S)C2, and BSCB1(R)C14. Four populations [BS16(S)C2, BS28(R)C3, BS29(R)C3, and BS34(S)C4] are exotic populations adapted to the temperate U.S. Corn Belt. BS16(S)C2 and BS28(R)C3 are included within the Stiff-Stalk Synthetic (BSSS) heterotic group and BS29(R)C3 and BS34(S)C4 are included in the Non-Stiff-Stalk Synthetic (non-BSSS) heterotic group.

Four sets of paired rows of all possible 35 crosses (seven BSSS populations crossed to five non-BSSS populations) were planted in the breeding nursery. Hand pollinations were done in both directions to develop the cross and a reciprocal cross between each paired row set with no plant being used more than twice as a pollen parent. The direction of the pollination allowed each cross to represent a distinct entry for a total number of crosses in the study equaling 70. Twenty  $F_1$  ears from each nursery row were harvested and combined with the other three rows representing the same cross for a total of 80  $F_1$  ears for each four-paired row set. The crosses and the reciprocal crosses were harvested and shelled separately. The 80  $F_1$  ears from each entry were shelled in bulk, the seed stirred, and then a bulk sample of  $F_1$  seed was taken to represent each particular cross (entry).

During the summer of 2002, the 70 population crosses, the 12 original parents, and 18 checks for a total of 100 entries were evaluated for agronomic performance in a 10 X 10 row-

column double lattice. The experiment was conducted at seven Iowa locations with three replications of the experiment at each location. The seven locations representing southern and central Iowa climatic conditions were: Ames, Ankeny, Carroll, Crawfordsville, Fairfield, Lewis, and Rippey, Iowa. Modern agricultural field plot planting equipment was used to plant all locations. Planting dates of the experiment ranged from the last week of April to the first week of May across all locations. In the experiment, each entry, or plot, was planted in two rows, 5.45 meters (18 feet) long with 0.75 meters (30 inches) between the rows. The plots were overplanted with 72 plants per plot and then thinned to 50 plants per plot for a final stand population of 24,200 plants per acre (59,798 plants per hectare). Conventional fertilization and weed control practices recommended for optimum maize production were used at all locations. Plots were machine harvested at all locations except Lewis.

Data for agronomic performance traits were collected for grain yield, stand, root lodging, stock lodging, and grain moisture at six of the seven locations. Mid-season drought conditions and insect infestations caused the experiment at the Lewis location to be discarded early in the summer. Plant and ear height data were collected at only Ames, Ankeny, and Crawfordsville, while pollen and silk data were collected only at the Ames location. A brief description of each trait is provided.

1. Yield was recorded as the total amount of shelled grain that was harvestable with a plot combine. The harvested grain in each plot was adjusted to  $155 \text{ g kg}^{-1}$  grain moisture (15.5% grain moisture) and converted to tonnes/hectare ( $\text{t ha}^{-1}$ ).
2. Grain moisture is the percent (%) grain moisture content of the shelled grain at harvest as measured by a moisture meter on the plot combine.
3. Stand is the number of plants per plot converted to plants per hectare ( $\text{p ha}^{-1}$ ). Stand counts were taken during the thinning period.
4. Root lodging is the percentage (%) of plants in a plot that were inclined more than 30 degrees ( $^{\circ}$ ) from vertical divided by the total number of plants in the plot.
5. Stock lodging is the percentage (%) of plants broken below the ear divided by the total number of plants in the plot.
6. Plant height is the average height (cm) of 20 plants in the plot measured from ground level to the flag leaf.

7. Ear height is the average height (cm) of 20 plants in the plot measured from ground level to the primary ear node.
8. Date of silk is the date when 50% of the plants in a plot had extruded silks and was recorded as the number of days after planting.
9. Date of pollen shed is the date when 50% of the plants in a plot had tassels shedding pollen and was recorded as the number of days after planting.

### Statistical Analysis Methods

A 10 x 10 row-column lattice experimental design was used to evaluate the experiment at each individual location. Lattice designs belong to a category of designs called incomplete block designs in which treatments are grouped into blocks that are not large enough to contain all treatments. Row-column lattice design classification allowed the experimental design to use two blocking criteria (i.e., rows and columns) to estimate block effects due to soil gradients within the field, and allowing treatment means to be adjusted for differences among blocks. Lattice designs are also resolvable designs in which they can be analyzed as a randomized complete block design (RCBD), since each treatment occurs once in each replicate. However, treatment mean adjustment based on intrablock effects is lost as a consequence of using the RCBD. In this study, calculation of the relative efficiency of the lattice design compared with the RCBD showed the lattice design more effective in adjusting means for field variation.

The linear model describing the row-column lattice design used to determine entry differences for each trait at each individual environment was as followed:

$$Y_{ijlm} = \mu + B_i + R_{j(i)} + C_{l(i)} + T_m + e_{ijlm},$$

where:

$Y_{ijlm}$  = the  $ijlm^{\text{th}}$  observation;

$\mu$  = the overall mean;

$B_i$  = the effect of the  $i^{\text{th}}$  replication;

$R_{j(i)}$  = the effect of the  $j^{\text{th}}$  row within the  $i^{\text{th}}$  replication;

$C_{l(i)}$  = the effect of the  $l^{\text{th}}$  column within the  $i^{\text{th}}$  replication;

$T_m$  = the effect of the  $m^{\text{th}}$  entry; and

$e_{ijlm}$  = the error effect associated with  $ijl(m)^{\text{th}}$  observation.

The expected mean squares derived for one trait at one location is shown in Table 1. The individual environment analysis of variance was done using the mixed model procedure (PROC MIXED) of SAS version 8.0. In the analysis of variance, entries were considered fixed effects and rows within replications, columns within replications, and locations considered as random effects. Individual environment phenotypic data were corrected for outliers; with outliers being considered data values two-and-a-half standard deviations from the mean being removed. Entry least-squares means (lsmeans) for each trait at each environment were computed from plot data and adjusted for row and column effects using the methodology outlined by Cockran and Cox (1992). An effective error mean square term (EEMS) was also obtained for each trait in every environment. The EEMS term was formed by determining the standard error of the difference for each possible pairwise entry comparison. Each standard error was squared, multiplied by the number of replications used to develop each entry mean, and averaged by dividing the term by two. All entry and replication differences were tested with the effective error mean square term.

Table 1. Analysis of variance with sources of variation, degrees of freedom (df), mean squares (MS), and expected mean squares (EMS) for one trait at one environment.

Source of variation	df		MS	EMS
Replications (R)	$(r - 1)$	2	$MS_3$	$\sigma_e^2 + g\sigma_R^2$
Columns (Q) (unadjusted) / R	$r(q-1)$	27		
Rows (P) (unadjusted) / R	$r(p-1)$	27		
Entries	$(g-1)$	99	$MS_2$	$\sigma_e^2 + r\phi_G$
Effective error mean square (EEMS)	$r(p-1)(q-1) - (g-1)$	144	$MS_1$	$\sigma_e^2$
Total	$rt-1$	299		

The combined analysis of variance for data combined across six environments was conducted using entry means adjusted for row and column effects from each individual environment analysis. The combined environment analysis was completed using PROC GLM of SAS version 8.0 using the following linear model:

$$Y_{ijk} = \mu + E_i + T_j + ET_{ij} + \text{pooled error},$$

where:

$Y_{ijk}$  = the  $ijk^{\text{th}}$  observation;

$\mu$  = the overall mean;

$E_i$  = the effect of the  $i^{\text{th}}$  environment;

$T_j$  = the effect of the  $j^{\text{th}}$  entry;

$ET_{ij}$  is the interaction effect between the  $i^{\text{th}}$  environment and the  $j^{\text{th}}$  entry; and pooled error is the error effect associated with  $ij(k)^{\text{th}}$  observation.

In the combined data analysis, environments and the environment x entry interaction were considered as random sources of variation while entries were considered as fixed sources of variation. The expected mean squares for the combined data analysis are shown in Table 2. Entry sums of squares were partitioned into among checks, among crosses, among parents, and the non-orthogonal comparisons of crosses verses checks and crosses verses parents. The contrast, crosses verses parents, provides an estimate of average heterosis among the crosses. Further partitioning of crosses sums of squares was based on the parameter of which parent, whether a Stiff-Stalk parent or a Non-Stiff-Stalk parent was used as the male or the female in the cross. This allowed the inclusion of reciprocal crosses to be analyzed within the study. Reference should be noted that partitioned population cross effects consider the 70 population crosses between different Stiff-Stalk and Non-Stiff-Stalk parents. The total number of population crosses, 70, includes 35 crosses where the Stiff-Stalk parent serves as the female parent in the cross (these population crosses will be hereafter referred to as Design II or (A x B) crosses) and 35 population crosses in which the Non-Stiff-Stalk parent serves as the female parent in the cross (these population crosses will be hereafter be referred to as Reciprocal Design II or (B x A) crosses). Sums of squares equations are listed and written out in Appendix G. The first two sums of squares partitions of crosses, Stiff-Stalk and Non-

Table 2. Analysis of variance with sources of variation, degrees of freedom (df), mean squares (MS), and expected mean squares (EMS) combined across environments.

Source of variation	df	MS	EMS
Environments (E)	(e-1)	5	$\sigma_e^2 + \sigma_{GE}^2 + g\theta_E$
Replications (R)/ E	e(r - 1)	12	
Columns (Q) / R / E	er(q-1)	162	
Rows (U) / R / E	er(u-1)	162	
Entries (G)	(g-1)	99 M3	$\sigma_e^2 + \sigma_{GE}^2 + e\theta_G$
Checks (CH)	(ch-1)	11 M31	$\sigma_e^2 + \sigma_{CH}^2 + e\theta_{CH}$
Crosses (C)	(c-1)	69 M32	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_C$
Stiff Stalk{SS} (S)	(s-1)	6 M321	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_{SE}$
Non-Stiff Stalk{NSS} (N)	(n-1)	4 M322	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_{NE}$
SS x NSS	(s-1)(n-1)	24 M323	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_{SNE}$
SS Female vs. SS Male	1	1 M324	$\sigma_e^2 + \sigma_{CE}^2 + e\sigma_{(SFvsSM)}^2$
SS {Maternal} (A)	(a-1)	6 M325	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_A$
NSS {Maternal} (B)	(b-1)	4 M326	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_B$
Reciprocal	(a-1)(b-1)	24 M327	$\sigma_e^2 + \sigma_{CE}^2 + e\theta_{AB}$
Parents (P)	(p-1)	17 M33	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_P$
Cycle 0 – C0 (CO)	(co-1)	5 M331	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_{CO}$
SS C0 (L)	(l-1)	2 M3311	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_M$
NSS C0 (M)	(m-1)	2 M3312	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_M$
SS C0 vs. NSS C0	1	1 M3313	$\sigma_e^2 + \sigma_{PE}^2 + e\sigma_{(SCOvsNCO)}^2$
Cycle I – CI (CI)	(ci-1)	11 M332	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_{CI}$
SS CI (J)	(j-1)	6 M3321	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_J$
NSS CI (K)	(k-1)	4 M3322	$\sigma_e^2 + \sigma_{PE}^2 + e\theta_K$
SS CI vs. NSS CI	1	1 M3323	$\sigma_e^2 + \sigma_{PE}^2 + e\sigma_{(SCHvsNSCI)}^2$
CI vs. C0	1	1 M333	$\sigma_e^2 + \sigma_{PE}^2 + e\sigma_{(COvsCI)}^2$
C vs. Ch	1	1 M34	$\sigma_e^2 + \sigma_{(CvsCH)E}^2 + e\sigma_{(CvsCH)}^2$
C vs. P	1	1 M35	$\sigma_e^2 + \sigma_{(CvsP)E}^2 + e\sigma_{(CvsP)}^2$

Table 2. (continued)

Source of Variation	df	MS	EMS
Entries x E	(g-1)(e-1)	495 M2	$\sigma_e^2 + \sigma_{GE}^2$
Checks x E	(ch-1)(e-1)	55 M21	$\sigma_e^2 + \sigma_{CH}^2$
Crosses x E	(c-1)(e-1)	345 M22	$\sigma_e^2 + \sigma_{CE}^2$
Parents x E	(p-1)(e-1)	85 M23	$\sigma_e^2 + \sigma_{PE}^2$
[(C vs. CH) x E]	1(e-1)	5 M24	$\sigma_e^2 + \sigma_{(CvsCH)E}^2$
[(C vs. P) x E]	1(e-1)	5 M25	$\sigma_e^2 + \sigma_{(CvsP)E}^2$
Pooled Error (EEMS)	$[e\{[(r-1)(g-1)] - \{(q-1)r\} + \{(u-1)r\}\}]/r$	864 MS <sub>1</sub>	$\sigma_e^2$
Total	(erg-1)	1799	

Stiff-Stalk, considers the 35 population crosses of both designs and were calculated by taking the average difference between each Design II cross and the Reciprocal Design II cross independently for both parental groups and subtracting that average difference by the overall average mean difference between the Design II crosses and the Reciprocal Design II crosses. These two partitioned effects provide an overall estimate of general combining ability for both the Stiff-Stalk and Non-Stiff Stalk heterotic groups. The interaction of Stiff-Stalk parents and Non-Stiff-Stalk parents provides an overall estimate of the specific combining ability between the two groups. An orthogonal comparison between Stiff-Stalk females verses Stiff-Stalk males was calculated by comparing the overall mean of the crosses when Stiff-Stalk parents were used as females in Design II crosses to the overall mean of crosses when Stiff-Stalk parents were used as males in Reciprocal Design II crosses. This orthogonal comparison determines if the Stiff-Stalk parent performs better as a female parent compared with its cross performance when used as a male parent.

The next two cross sums of squares partitions describe reciprocal effects of both parental groups based upon reciprocal cross analysis. The Stiff-Stalk maternal effect and the Non-Stiff-Stalk maternal effect were calculated by taking one-half the difference between the average performance of a Design II parent verses the average performance of the same parent in the Reciprocal Design II. These two effects provided an estimate of GCA for the

reciprocal crosses. The reciprocal effect sums of square partition was calculated based on the deviation of the mean for a specific cross from the predicted value based on Stiff-Stalk maternal, Non-Stiff-Stalk maternal, and the reciprocal cross effects. The reciprocal cross effect provides an estimate of SCA for the reciprocal crosses. A second separate analysis considering only the reciprocal effect also was done to estimate the overall difference between the Design II crosses and the Reciprocal Design II crosses. This effect combines the Stiff-Stalk maternal effect, the Non-Stiff-Stalk maternal effect, and the reciprocal effect together and was calculated by taking one-half of the difference between a population cross occurring in the Design II mating design and the same population cross occurring in the Reciprocal Design II mating design.

The among parents sums of squares were also partitioned further into Cycle 0 parents (original population before recurrent selection), and into Cycle *I* parents (the population after *I* cycles of recurrent selection) which were used to make the Design II and the Reciprocal Design II crosses. Each cycle was sub-partitioned into Stiff-Stalk, Non-Stiff-Stalk parents, along with three orthogonal comparisons being preformed in which Stiff-Stalk Cycle 0 parents were compared against Non-Stiff-Stalk Cycle 0 parents, Stiff-Stalk Cycle *I* parents were compared against Non-Stiff-Stalk Cycle *I* parents and Cycle *I* parents were compared against Cycle 0 parents. A third separate analysis considering contrasts between Cycle *I* parents and Cycle 0 parents also was completed to determine the success recurrent selection has had in population improvement from the original Cycle 0 parent to the Cycle *I* parent used in population cross development.

The entry x environment term was partitioned only into the following effects: checks x environment, crosses x environment, parents x environment, and the two non-orthogonal comparisons: (crosses vs. checks) x environments, and (crosses vs. parents) x environments. Further complete interaction partitioning was eliminated from the analysis to prevent having multiple error terms, some with few degrees of freedom, being used to test significance among the different sources of variation.

In the combined analysis, replications within environments, columns within replications within environments, and rows within replications within environments were listed in Table 2 to show all possible degrees of freedom, but were left out of the calculated



expected mean squares and as part of the total variation present because individual environment means, already adjusted for replication, row, and column effects, were used in the combined analysis.

F-tests were computed to determine significance among different sources of variation and their partitioned effects within the combined analysis. The environment x entry interaction term was used to test both the environment and the entry sources of variation. Environment x entry interaction partitioned effects were used to test the corresponding partitioned entry effects. The parent x environment effect was used to determine significance among the different parent population comparisons. A pooled effective error mean square (pooled EEMS) term was used to test the environment x entry interaction and the interaction's partitioned effects. Calculation of the pooled EEMS term was done as follows:

- 1) The EEMS term computed for each trait in the individual environment analysis was multiplied by its corresponding degrees of freedom (df) to obtain an effective error sums of squares (EESS) term.
- 2) Then for each trait a pooled effective error sums of squares (pooled EESS) term was created by the summation of the EESS terms over the six environments used in the study.
- 3) A pooled degrees of freedom (pooled df) term was also created by the summation of the df over the six environments.
- 4) The pooled EESS term was then divided by the pooled df term to derive the pooled EEMS term on an observation basis for each trait.
- 5) Finally, to get the EEMS term from an observation basis to a means basis, the EEMS term was divided by the number of replications at each environment within the study.

Estimation of heterosis among crosses was only done by estimation of mid-parent heterosis. Mid-parent heterosis calculations are based on the difference between the  $F_1$  cross and the mid-parent value and are also calculated based on percentages. These estimates were calculated using combined means over environments for all cross entries. The formulas used to calculate both heterosis values were included within the literature review.

## RESULTS AND DISCUSSION

### Examination of Combined Analysis Mean Squares

The combined analysis of variance summarizes the results for the nine traits investigated within this Design II study (Table 3). In the analysis, highly significant differences ( $Pr \leq 0.01$ ) were detected among entries for all traits studied over more than one environment. The traits pollen date and silk date were only studied at one environment, so environmental differences were not reported. These significant environmental differences reported resulted from large day-to-day weather differences that occurred at each separate environment used in this study throughout the 2002 growing season. The 2002 growing season was characterized as having a cool, wet spring, followed by a summer that had unusually high temperatures and low levels of precipitation. High day time temperatures followed by the above normal evening temperatures allowed for the accumulation of 2930 growing degree days around the Ames area based on meteorological data (Herzmann and Arritt, 2003) necessary for adequate crop growth. However, due to the summer month's dry and hot weather, insect problems also prevailed causing detrimental effects at some environments in which the study was conducted. Despite adverse summer drought and insect problems, record grain yields were recorded, much to the surprise of most grain producers, throughout the state.

Because highly significant differences were detected among entries for all traits evaluated in the study, entries were partitioned for further analysis into the following categories: among checks; among crosses; among parents; and into two non-orthogonal one degree of freedom comparisons (crosses verses checks, and crosses verses parents). Check entries were placed into the study to reference how well the hybrid population crosses preformed compared with the elite hybrids that are currently being used by grain producers. Highly significant differences ( $Pr \leq 0.01$ ) were observed among checks for all traits except for stand. A similar pattern was observed among the 70 population crosses, in which significant differences were detected for all traits except for stand. The occurrence of no significant differences in stand among crosses and among checks was due to plots being over-planted at planting time and then five weeks later being thinned back to a selected stand density.

Table 3. Analysis of variance of eight traits evaluated on 70 Design II crosses combined across six environments.

Sources of variation	Yield (t ha <sup>-1</sup> )		Moisture (%)		Stand (plants ha <sup>-1</sup> )		Root Lodging (%)	
	df	Mean Square	df	Mean Square	df	Mean Square	df	Mean Square
Environments (E)	5	76.78**	5	888.05**	5	10.0**	5	8346.0**
Entries (G)	99	10.10**	99	9.05**	99	38.6**	99	314.3**
Checks (CH)	11	28.49**	11	12.56**	11	0.9	11	278.2**
Crosses (C)	69	2.48**	69	6.25**	69	0.4	69	206.2**
Stiff Stalk{SS} (S)	6	18.99**	6	28.60**	6	0.8	6	1445.0**
Non-Stiff Stalk{NS}(N)	4	7.91**	4	58.37**	4	0.3	4	456.7**
SS x NSS	24	0.61**	24	0.65**	24	0.5	24	78.9
SS Female vs. SS Male	1	0.47	1	0.01	1	0.1	1	89.4
SS {Maternal} (A)	6	0.66*	6	0.33	6	0.3	6	51.2
NSS {Maternal} (B)	4	0.07	4	0.37	4	0.4	4	50.6
Reciprocal	24	0.26	24	0.29	24	0.2	24	51.6
Parents (P)	17	5.49**	17	12.57**	17	187.5**	17	615.0**
Cycle 0 – C0 (C0)	5	4.17**	5	10.24**	5	460.6**	5	447.1*
SS C0 (L)	2	6.38**	2	1.05	2	462.3**	2	751.2*
NSS C0 (M)	2	0.81*	2	19.26**	2	689.3**	2	130.6
SS C0 vs. NSS C0	1	6.52**	1	10.54**	1	0.0	1	134.8
Cycle I – CI (CI)	11	3.48**	11	14.36**	11	21.2*	11	629.2**
SS CI (J)	6	3.85**	6	15.97**	6	30.5*	6	1013.7**
NSS CI (K)	4	3.77**	4	15.54**	4	11.1	4	188.0
SS CI vs. NSS CI	1	0.07	1	0.01	1	6.1	1	86.6
CI vs. C0	1	34.25**	1	4.66**	1	650.3**	1	1636.1**
C vs. Ch	1	0.09	1	112.56**	1	1.9	1	3027.6**
C vs. P (Cycle I)	1	194.61**	1	0.02	1	47.5*	1	202.8

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

† Plant height measured at three locations.

‡ Ear height measured at three locations.

§ Pollen date measured at one location.

¶ Silk date measured at one location

Stalk Lodging (%)		Plant Height† (%)		Ear Height‡ (cm)		Pollen Date§ (days)		Silk Date¶ (days)	
Mean		Mean		Mean		Mean		Mean	
df	Square	df	Square	df	Square	df	Square	df	Square
5	1788.9**	3	6558.0**	3	2880.9**				
99	91.5**	99	484.0**	99	238.2**	99	3.69**	99	4.05**
11	52.6**	11	972.1**	11	399.4**	11	15.85**	11	12.83**
69	57.1**	69	207.0**	69	92.8**	69	1.65**	69	1.76**
6	350.4**	6	847.0**	6	282.8**	6	3.65**	6	5.44**
4	143.6**	4	1580.8**	4	766.5**	4	14.27**	4	9.57**
24	26.8*	24	54.8**	24	29.4*	24	0.91**	24	1.02**
1	0.0	1	0.9	1	1.0	1	0.39	1	1.98
6	13.9	6	67.8*	6	18.3	6	0.66	6	0.45
4	8.1	4	113.1**	4	95.4**	4	0.46	4	0.61
24	20.9	24	29.4	24	18.5	24	0.30	24	0.80
17	171.1**	17	583.9**	17	447.8**	17	2.62**	17	3.91**
5	49.5	5	168.9**	5	300.0**	5	1.92**	5	5.61**
2	25.8	2	76.7	2	27.2	2	1.51	2	0.89
2	86.6	2	293.8**	2	718.0**	2	2.99**	2	13.12**
1	22.5	1	103.5	1	9.5	1	0.58	1	0.02
11	128.1**	11	657.5**	11	373.9**	11	3.18**	11	2.67**
6	164.6**	6	638.7**	6	347.6**	6	1.99**	6	2.49**
4	94.6*	4	674.2**	4	452.9**	4	5.72**	4	3.59**
1	43.4	1	703.9**	1	215.1**	1	0.18	1	0.11
1	1251.4**	1	1849.3**	1	1999.8**	1	0.01	1	8.92**
1	446.2**	1	10050.7*	1	4988.4**	1	24.30*	1	40.21*
1	46.4	1	6881.4**	1	2075.8**	1	2.55	1	4.76

Table 3. (cont)

Sources of Variation	Yield (t ha <sup>-1</sup> )		Moisture (%)		Stand (plants ha <sup>-1</sup> )		Root Lodging (%)	
	df	Mean Square	df	Mean Square	df	Mean Square	df	Mean Square
Entries x E	495	0.27**	495	0.28**	495	2.5**	495	100.8**
Checks x E	55	0.44**	55	0.37**	55	1.1*	55	80.2**
Crosses x E	345	0.24**	345	0.21**	345	0.4	345	79.8**
Parents x E	85	0.24**	85	0.35**	85	10.5**	85	188.7**
[(C vs. CH) x E]	5	1.01**	5	2.17**	5	1.2**	5	183.1**
[(C vs. P) x E]	5	0.31	5	0.45**	5	6.3**	5	204.7**
Pooled Error (EEMS)	842	0.15	853	0.14	864	0.8	854	46.9
<u>Combined Analysis</u>								
Mean		6.57		19.62		59.16		24.77
CV(%)		7.94		2.67		2.68		40.53
LSD <sub>(0.05)</sub> #		0.59		0.60		1.80		11.38

# Least significant difference at the 0.05 significance level, respectively.

Stalk Lodging (%)		Plant Height (cm)		Ear Height (cm)		Pollen Date (days)		Silk Date (days)	
Mean		Mean		Mean		Mean		Mean	
df	Square	df	Square	df	Square	df	Square	df	Square
495	19.0**	198	31.9**	198	17.3**				
55	9.3	22	62.7**	22	25.3*				
345	16.3**	138	25.3**	138	17.2**				
85	34.0**	34	27.7	34	13.0				
5	17.8	2	155.5**	2	3.1				
5	23.1	2	16.4	2	6.2				
857	13.5	432	22.1	432	15.1	144	0.51	144	0.53
	8.46		228.45		108.75		71.74		73.92
	51.46		2.47		3.82		1.00		1.00
	4.94		9.10		6.70		1.14		1.17

Population crosses showing significant differences were further partitioned into the following categories: Stiff-Stalk crosses; Non-Stiff-Stalk crosses; the interaction of Stiff-Stalk crosses by Non-Stiff-Stalk crosses; a one degree of freedom comparison of the Stiff-Stalk parent being used as a female compared with the Stiff-Stalk parent being used as a male; a Stiff-Stalk maternal effect; a Non-Stiff-Stalk maternal effect; and a reciprocal effect corresponding to the interaction between the Stiff-Stalk maternal effect and the Non-Stiff-Stalk maternal effect. Again, reference should be noted that these partitioned effects include the 70 population crosses between different Stiff-Stalk and Non-Stiff-Stalk parents. The 70 population crosses include 35 crosses where the Stiff-Stalk parent served as the female parent in the cross (now referred to as Design II or (A x B) crosses) and 35 population crosses in which the Non-Stiff-Stalk parent served as the female parent in the cross (now referred to as Reciprocal Design II or (B x A) crosses).

The first two partitioned effects among crosses, Stiff-Stalk crosses and Non-Stiff-Stalk crosses both showed highly significant differences among all traits except for stand (Table 3). These two partitioned effects consider all 70 population crosses in both designs and were calculated by taking the average difference between each Design II cross and the Reciprocal Design II cross and subtracting the average difference between the Design II cross total and the Reciprocal Design II cross total. These effects provide overall GCA estimates based on both designs for both the Stiff-Stalk and the Non-Stiff-Stalk parents. The interaction of Stiff-Stalk crosses by Non-Stiff-Stalk crosses had highly-significant differences being detected for grain yield, grain moisture, plant height, pollen date, and silk date; while only a significant difference ( $Pr \leq 0.05$ ) was reported for stalk lodging and plant ear height. This partitioned effect provided an overall estimate of SCA for Stiff-Stalk by Non-Stiff-Stalk crosses. No significant differences were detected among all traits evaluated for by the orthogonal comparison of Stiff-Stalk female verses Stiff-Stalk male in which the overall mean of Design II crosses was compared with the overall mean of Reciprocal Design II crosses.

The next two cross partitioned effects, a Stiff-Stalk maternal effect and a Non-Stiff-Stalk maternal effect, consider the inclusion of reciprocal crosses in order to examine maternal effects and were calculated as one-half the difference between a Design II cross

parent mean and a Reciprocal Design II cross parent mean. These estimates provided a GCA estimate for reciprocal effects between the two types of design II crosses. Research studies have shown though that nongenetic maternal effects can usually be assumed absent for the estimation of components of genetic variances within a maize (*Zea mays* L.) population (Comstock and Robinson, 1952). Therefore, since maternal and reciprocal effects are assumed to be absent or small in maize, reciprocal crosses are usually not grown in most studies (Hallauer and Martinson, 1975). However, reciprocal crosses in this study showed significant differences being detected for grain yield and plant height for the Stiff-Stalk maternal effect, while highly significant differences were detected only for plant height and plant ear height traits for the Non-Stiff-Stalk maternal source of variation. Finally, the last cross partitioned effect, the reciprocal effect, serves as the interaction effect between the Stiff-Stalk maternal effect and the Non-Stiff-Stalk maternal effect and is a estimate of SCA for reciprocal effects between crosses. No significant differences ( $Pr \geq 0.05$ ) were detected among all the traits evaluated for reciprocal effects.

Crosses were partitioned differently for a second separate analysis (mean squares not shown) in which the Stiff-Stalk maternal effect, the Non-Stiff-Stalk maternal effect, and the reciprocal effect were combined together to form only a reciprocal effect. Statistically significant reciprocal effect differences were detected for grain moisture, plant height, and ear height. This effect calculated the mean difference among traits evaluated by taking one-half the mean difference between a Design II cross and a Reciprocal Design II cross. The reciprocal effect estimates will be reported to determine if reciprocal differences between the Design II crosses and the Reciprocal Design II crosses were significant.

The parents mean square was highly significant for all traits and was further partitioned into Cycle 0 and Cycle I parents along with a one degree of freedom comparison of Cycle I parents vs. Cycle 0 parents (Table 3). Highly significant differences were detected among Cycle 0 parents for all traits except stalk lodging. The Stiff-Stalk Cycle 0 partition showed significant differences for yield ( $Pr \leq 0.01$ ), stand ( $Pr \leq 0.01$ ), and root lodging ( $Pr \leq 0.05$ ), while the Non-Stiff-Stalk Cycle 0 partition showed a significant difference ( $Pr \leq 0.05$ ) for grain yield and highly significant differences ( $Pr \leq 0.01$ ) for moisture, stand, plant height, ear height, pollen date and silk date. A one degree of freedom orthogonal comparison



between Stiff-Stalk Cycle 0 parents and Non-Stiff-Stalk Cycle 0 parents showed highly significant differences only among the traits grain yield and grain moisture.

The Cycle *I* mean square was highly significant for all traits except stand, for which only a significant difference was detected. A similar pattern of significant differences was found among the Stiff-Stalk Cycle *I* partition. The Non-Stiff-Stalk Cycle *I* parents mean square was highly significant for grain yield, grain moisture, plant height, ear height, pollen date, and silk date; while only a significant difference was detected for stalk lodging. The contrast, Stiff-Stalk Cycle *I* parents verses Non-Stiff-Stalk Cycle *I* parents, showed highly significant differences only for the traits plant and ear height. Finally, the orthogonal one degree of freedom comparison, Cycle *I* parents verses Cycle 0 parents showed highly significant differences for all traits except pollen date.

The single degree of freedom, non-orthogonal comparison of parents verses crosses, which is a test of average heterosis, was found to be statistically different from zero for grain yield and ear height ( $Pr \leq 0.01$ ), and plant height ( $Pr \leq 0.05$ ). This contrast implies that non-additive effects were important for these traits. Crosses were not significantly different from parents *per se* for grain moisture, root lodging, stalk lodging, pollen date, and silk date. The final non-orthogonal single-degree of freedom comparison of crosses verses checks showed significant differences for the agronomic traits grain moisture, root lodging, stalk lodging, plant height, ear height, pollen date and silk date. No significant differences ( $Pr \leq 0.05$ ) were reported for the traits grain yield and stand.

The entries by environment source of variation showed highly significant differences for all traits evaluated within the study. This significant source of variation was further partitioned into the following interaction categories: checks by environment; crosses by environment; parents by environment; and the two comparisons: (crosses verses checks) by environments and (crosses verses parents) by environments. The mean squares of most of these partitioned effects showed highly significant or statistically significant differences for most all of the traits evaluated in the study (Table 3). However, due to the highly significant nature of the entry by environment interaction for all the traits evaluated over multiple environments, further discussion will focus only on the combined data analysis. The trait

‘Stand’ will not be discussed because no significant differences occurred for all cross partitions due to thinning early in the growing season.

### **Individual Trait Analysis**

**Grain Yield:** Grain yield means for the 35 Design II (A x B) crosses and the 35 Reciprocal Design II (B x A) crosses between Stiff-Stalk and Non-Stiff-Stalk populations averaged across six locations are presented in Table 4 and Table 5. Tables 4 and 5 also include the grain yield means of the 12 parent populations *per se* used to develop the population crosses for this study and will be discussed next in detail.

Grain yield means of the Stiff-Stalk parent populations *per se* ranged from 4.11 t ha<sup>-1</sup> for BS34(S)C4 to 6.77 t ha<sup>-1</sup> for BS10(FR)C14, whereas the Non-Stiff-Stalk parent populations had grain yield means that ranged from 3.88 t ha<sup>-1</sup> for BSCB1(R)C14 to 5.83 t ha<sup>-1</sup> for BS11(FR)C14. Differences between the highest yielding and the lowest yielding parent populations for both groups of parents were greater than the least significant difference value at the five percent level of significance (LSD<sub>0.05</sub>) of 0.56 t ha<sup>-1</sup>. This confirms the results of the combined environment analysis (Table 3) showing significant differences existing in grain yield for both Cycle I Stiff-Stalk and Cycle I Non-Stiff-Stalk parent populations. Overall, the Cycle I parents had an average grain yield of 5.18 t ha<sup>-1</sup> (Table 6).

Based on parent grain yields, the Non-Stiff-Stalk population BS11(FR)C14 and the Stiff-Stalk population BS10(FR)C14 had the two highest parent yields of 5.83 t ha<sup>-1</sup> and 6.77 t ha<sup>-1</sup> after 14 cycles of full-sib reciprocal recurrent selection (Table 4). However, the Stiff-Stalk population BSSS(R)C14 and the Non-Stiff-Stalk population BSCB1(R)C14, complementing each other through 14 cycles of reciprocal recurrent selection, had lower than average grain yields of 4.86 t ha<sup>-1</sup> and 3.88 t ha<sup>-1</sup>. These grain yield values were significantly different from BS11(FR)C14 and BS10(FR)C14 using the LSD<sub>0.05</sub> listed earlier. Echandi and Hallauer (1996) reported similar parent means in a diallel study, which included the aforementioned four U.S. Corn Belt populations.

Adequate grain yield levels were maintained by the four adapted tropical cultivars. Grain yields of BS16(S)C2, BS28(R)C3, BS29(R)C3, and BS34(S)C4 were similar to some of the more advanced U.S. Corn Belt populations included in recurrent selection programs.

Table 4. Grain yield of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

12 populations per 30 using combined environment means										
Populations		SS Females (A)‡								
		----- U.S. Corn Belt -- (1)§ -----					- Adapted Exotic -- (2) -			
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- t ha <sup>-1</sup> -----								
BS11(FR)C14	(1)	7.68	7.40	7.23	7.07	7.39	7.38	6.59	7.25	5.83
BS26(S)C4	(1)	7.24	7.32	6.38	6.27	7.51	6.58	5.47	6.68	5.16
BSCB1(R)C14	(1)	7.60	7.58	6.96	6.94	7.53	6.93	6.34	7.13	3.88
BS16(S)C2	(2)	7.18	6.78	6.46	6.61	6.96	6.13	5.74	6.55	5.07
BS29(R)C3	(2)	8.03	7.43	6.60	6.77	7.91	6.34	6.23	7.04	5.80
Average		7.55	7.30	6.73	6.73	7.46	6.67	6.07	6.93	5.15
Parent mean		6.77	5.26	5.32	5.20	4.86	4.96	4.11	5.21	5.19

† LSD<sub>(0.05)</sub> is 0.56 t ha<sup>-1</sup> for both crosses and parents *per se* within the crosses. Check grain yield mean: LH198 x LH185 = 9.66 t ha<sup>-1</sup>.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table 5. Grain yield of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
	NSS Females (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- t ha <sup>-1</sup> -----								
BS11(FR)C14	(1)	7.44	8.00	7.05	7.49	7.68	6.68	7.09	7.35	5.83
BS26(S)C4	(1)	7.24	7.44	6.71	6.09	7.35	6.41	5.67	6.70	5.16
BSCB1(R)C14	(1)	7.41	7.86	7.13	6.53	8.04	6.96	5.95	7.13	3.88
BS16(S)C2	(2)	6.89	7.34	6.65	6.56	7.33	6.20	5.42	6.63	5.07
BS29(R)C3	(2)	7.89	7.82	7.10	7.10	7.92	6.23	6.22	7.18	5.80
Average		7.37	7.69	6.93	6.75	7.66	6.50	6.07	7.00	5.15
Parent mean		6.77	5.26	5.32	5.20	4.86	4.96	4.11	5.21	5.19

† LSD<sub>(0.05)</sub> is 0.56 t ha<sup>-1</sup> for both crosses and parents *per se* within the crosses. Check grain yield mean: LH198 x LH185 = 9.66 t ha<sup>-1</sup>.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table 6. Summary of means and average mid-parent and high-parent heterosis for Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) Design II and Reciprocal Design II population crosses, and parents *per se* for nine agronomic traits using combined environment means.

Group means	Grain yield	Grain moisture	Root lodging	Stalk lodging	Stand	Plant height†	Plant ear height	Pollen date‡	Silk date
	t ha <sup>-1</sup>	----- % -----			p ha <sup>-1</sup> (x 1000)	----- cm -----		---- days ----	
<u>Crosses</u>									
Design II§									
Stiff-Stalk (SS) females x Non-Stiff-Stalk (NSS) males	6.93	19.8	25.5	8.1	59.7	233.1	111.4	72.0	73.8
Reciprocal Design II¶									
Stiff-Stalk (SS) males x Non-Stiff-Stalk (NSS) females	7.00	19.8	25.0	8.2	59.7	232.6	110.9	71.8	74.1
Mean	6.97	19.8	25.3	8.2	59.7	232.9	111.1	71.9	74.0
<u>Parents</u>									
Cycle I									
Among Stiff-Stalk	5.21	19.8	22.7	8.4	58.5	213.9	100.7	72.4	74.7
Among Non-Stiff-Stalk	5.15	19.8	24.9	10.0	59.1	222.8	105.7	72.2	74.5
Mean	5.18	19.8	23.8	9.2	58.8	218.4	103.2	72.3	74.6
Cycle 0									
Among Stiff-Stalk	3.56	18.8	33.8	17.1	53.6	227.6	114.9	72.6	76.2
Among Non-Stiff-Stalk	4.42	19.9	30.0	15.5	53.6	232.4	116.4	72.0	76.1
Mean	3.99	19.4	31.9	16.3	53.6	230.0	115.7	72.3	76.1

† Plant height and plant ear height means averaged over three locations.

‡ Pollen date and silk date means averaged over one location.

§ Design II crosses produced using the Stiff-Stalk populations as females and Non-Stiff-Stalk populations as males.

¶ Reciprocal Design II crosses produced using Non-Stiff-Stalk populations as females and Non-Stiff-Stalk populations as males.

Table 6. (cont.)

Group Means	Grain yield	Grain moisture	Root lodging	Stalk lodging	Stand	Plant height	Plant ear height	Pollen date	Silk date
<u>Average mid-parent heterosis</u>									
<u>Crosses</u>	----- % -----								
Design II									
SS x NSS	33.78	0.0	7.2	-11.7	1.44	6.8	7.9	-0.5	-1.0
Reciprocal Design II									
NSS x SS	35.14	0.2	4.9	-10.9	1.47	6.5	7.5	-0.8	-0.7
Mean	34.55	0.1	6.1	-11.3	1.46	6.7	7.7	-0.6	-0.8

One example is the adapted tropical population, BS29(R)C3, which is listed under the Non-Stiff-Stalk group. BS29(R)C3 had a mean parent yield of  $5.80 \text{ t ha}^{-1}$  which was not significantly different to the highest yielding Non-Stiff-Stalk parent BS11(FR)C14, which had a mean parent yield of  $5.83 \text{ t ha}^{-1}$  (Table 4). Considering the Stiff-Stalk group, another example was seen with the adapted tropical population, BS28(R)C3, which had a parent grain yield mean of  $4.96 \text{ t ha}^{-1}$ . The BS28(R)C3 grain yield was not significantly different to a higher yielding Stiff-Stalk U.S. Corn Belt population BSK(S)C11 which had a parent mean yield of  $5.20 \text{ t ha}^{-1}$ .

The grain yield means of the adapted tropical populations confirm earlier results reported by Oyervides-García *et al.* (1985), San Vicente and Hallauer (1993), Echandi and Hallauer (1996), and Menz and Hallauer (1997) suggesting that the adapted tropical populations evaluated have achieved, in terms of agronomic grain yield performance, an adequate level of adaptation to U.S. Corn Belt conditions. The ability of these adapted tropical populations to perform in U.S. Corn Belt conditions have been considered important by Moll *et al.*, (1962) and Gerrish (1983) in order to obtain heterosis estimates that are unbiased between temperate and exotic germplasm and dismiss potential concern over inadequate racial sampling within the adapted tropical populations *per se*.

Cycle 0 populations (original populations) of the eight Stiff-Stalk and Non-Stiff-Stalk U.S. Corn Belt populations were also evaluated in this study (Table 7). Cycle 0 population grain yield means ranged from  $2.53 \text{ t ha}^{-1}$  for the Stiff-Stalk population BSKC0 to  $4.86 \text{ t ha}^{-1}$  for the Non-Stiff-Stalk population BS26C0. Significant differences between the highest and lowest yielding populations were detected based on the  $\text{LSD}_{0.05}$  of  $0.38 \text{ t ha}^{-1}$  estimated for yield. The six Cycle 0 parents included in the study had an average grain yield of  $3.99 \text{ t ha}^{-1}$  ( $63.4 \text{ bu acre}^{-1}$ ) compared with the average grain yield of  $5.18 \text{ t ha}^{-1}$  ( $82.9 \text{ bu acre}^{-1}$ ) for the populations undergoing recurrent selection (Table 6).

A separate analysis was done to estimate the difference between Cycle 1 and Cycle 0 U.S. Corn Belt populations to determine if recurrent selection programs had improved the mean grain yield performance of the populations *per se* (Table 8). Population improvement for increased grain yield was achieved in seven of eight populations evaluated. The

Table 7. Summary of means for Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) Cycle 0 parents for nine agronomic traits using combined environment means.

Parent/cycle comparisons	Parent type	Grain yield	Grain moisture	Root lodging	Stalk lodging	Stand†	Plant height‡	Plant ear height	Pollen date§	Silk date
		t ha <sup>-1</sup>	----- % -----			p ha <sup>-1</sup> (x 1000)	----- cm -----		---- days ----	
BS10C0	SS	4.59	18.5	24.1	16.8	58.4	222.3	111.6	71.8	75.2
BSSSC0	SS	3.56	18.6	31.4	19.3	58.9	232.3	115.6	72.0	76.2
BSKC0	SS	2.53	19.3	46.0	15.2	43.4	228.2	117.6	74.0	77.1
BS11C0	NSS	4.32	21.6	34.2	14.0	59.8	241.7	134.2	73.5	80.2
BS26C0	NSS	4.82	20.0	30.8	12.7	41.2	233.6	108.6	72.4	74.5
BSCB1C0	NSS	4.10	18.1	24.9	19.8	59.8	222.0	106.4	70.1	73.5
Average		3.99	19.4	31.9	16.3	53.6	230.0	115.7	72.3	76.1
LSD <sub>(0.05)</sub> ¶		0.38	0.9	18.9	6.5	5.2	10.4	7.1	1.1	1.2

† Plant height and plant ear height measured for three environments.

‡ Pollen date and silk date traits measured for one environment.

§ LSD<sub>(0.05)</sub> equals least significant difference at 0.05 percent significance level, respectively.



population BSCB1(R)C14, showed a  $0.23 \text{ t ha}^{-1}$  decrease in yield following 14 cycles of reciprocal recurrent selection. Martin and Hallauer (1980) reported similar results when growing the BSCB1 population between Cycle 0 ( $5.18 \text{ t ha}^{-1}$ ) and Cycle 7 ( $4.74 \text{ t ha}^{-1}$ ) showing a decrease of  $0.44 \text{ t ha}^{-1}$  in yield. This decrease could be the result of decreasing genetic variability and favorable allele selection accenting the yield trait following each successive cycle of reciprocal recurrent selection. Selection was based on testcrosses with BSSS(R); hence selection emphasized performance on the basis of testcrosses, rather than within population selection. Recurrent selection programs led to the greatest significant increases in yield for the populations BSK(HI)C11, BSK(S)C11, and BS10(FR)C14 ( $2.79$ ,  $2.66$ , and  $2.18 \text{ t ha}^{-1}$ , respectively) following 10 or more cycles of recurrent selection. These significant increases in yield suggest that genetic variability and the presence of favorable alleles are still present in the populations suggesting future incremental improvements in complex traits such as yield to be possible.

The 70 population crosses, with a mean grain yield of  $6.97 \text{ t ha}^{-1}$ , showed a 34.6 % improvement in grain yield over the 12 parents mean grain yield of  $5.18 \text{ t ha}^{-1}$  (Table 6). The 34.6 % improvement in grain yield represents an estimate of average heterosis between the crosses and the parents (Hallauer and Miranda, 1988). The 35 Design II crosses had an average cross grain yield mean of  $6.93 \text{ t ha}^{-1}$ , while the 35 Reciprocal Design II crosses had an average cross grain yield mean of  $7.00 \text{ t ha}^{-1}$ . The difference between the different cross design means was nonsignificant based on the  $\text{LSD}_{0.05}$  of  $0.56 \text{ t ha}^{-1}$ .

Among Design II  $F_1$  crosses the Stiff-Stalk populations BS10(FR)C14 ( $7.55 \text{ t ha}^{-1}$ ), BS13(S)C9 ( $7.30 \text{ t ha}^{-1}$ ), and BSSS(R)C14 ( $7.46 \text{ t ha}^{-1}$ ) had the highest yields in hybrid combination (Table 4). These three populations served as female parents in the Design II crosses. As for the male parents, or Non-Stiff-Stalk populations, the populations BS11(FR)C14 ( $7.25 \text{ t ha}^{-1}$ ) and BSCB1(R)C14 ( $7.13 \text{ t ha}^{-1}$ ) had the highest average grain yields while in hybrid combination. Considering the population crosses *per se*, the average grain yields ranged from a high of  $8.03 \text{ t ha}^{-1}$  for the cross BS10(FR)C14 x BS29(R)C3 to a low of  $5.47 \text{ t ha}^{-1}$  for the cross BS34(S)C4 x BS26(S)C4. The difference between the high and low population crosses exceeded the  $\text{LSD}_{0.05}$  of  $0.56 \text{ t ha}^{-1}$ , showing significant differences among the population crosses *per se*. A interesting result was that the highest

Table 8. Summary of different parent population comparisons for recurrent selection improvement between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) Cycle 1 parents and Cycle 0 parents following 'I' cycles of recurrent selection for nine agronomic traits using combined environment means.†

Parent/cycle comparisons	Parent type	Grain yield t ha <sup>-1</sup>	Grain moisture ----- % -----	Root lodging	Stalk lodging	Stand p ha <sup>-1</sup> (x 1000)	Plant height‡ ----- cm -----	Plant ear height	Pollen date§ ---- days ----	Silk date
BS10(FR)C14 vs. BS10C0	SS	2.18**	0.4	-5.8	-10.7**	1.3	8.5**	5.2*	2.0*	0.5
BS11(FR)C14 vs. BS11C0	NSS	1.51**	-3.5**	-6.8	-2.2	0.0	-7.4*	-25.4**	0.1	-5.5**
BS26(S)C4 vs. BS26C0	NSS	0.34	0.4	-12.8	1.3	15.5	4.8	7.9**	-0.2	1.7
BSCB1(R)C14 vs. BSCB1C0	NSS	-0.23	0.4	-0.3	-15.0**	0.0	-17.4**	-18.8**	1.8	-0.3
BSK(HI)C11 vs. BSKC0	SS	2.79**	0.7**	-15.7*	-4.9	16.3	-20.3**	-18.8**	-2.0*	-3.9**
BSK(S)C11 vs. BSKC0	SS	2.66**	0.3	-24.2**	4.5	16.2	-10.9*	-19.9**	-2.4*	-2.4*
BSSS(FR)C14 vs. BSSSC0	SS	1.30**	0.3	-15.1	-13.4	-4.9**	0.3	-6.6**	1.1	0.0
BS13(S)C9 vs. BSSSC0	SS	1.70**	0.2	-25.6**	-14.0	-1.8**	-41.1**	-31.9**	2.1*	-0.8

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard Errors (SE): Grain yield SE = 0.28; Grain moisture SE = 0.34; Root lodging SE = 7.93; Stalk lodging SE = 3.36; Stand SE = 1.87; Plant height SE = 3.04; Plant ear height SE = 2.08; Pollen date SE = 1.01; Silk date SE = 1.03;

‡ Plant height and plant ear height measured for three environments.

§ Pollen date and silk date traits measured for one environment.

yielding cross BS10(FR)C14 x BS29(R)C3, containing 50% adapted tropical germplasm, out-performed the highest yielding 100% U.S. Corn Belt germplasm cross of BSCB1(R)C14 x BS13(S)C9 on average by  $0.24 \text{ t ha}^{-1}$ . However, this difference in yield was not significant based on the  $\text{LSD}_{0.05}$ .

Among the Reciprocal Design II  $F_1$  crosses, the Stiff-Stalk populations BS13(S)C9 ( $7.69 \text{ t ha}^{-1}$ ) and BSSS(R)C14 ( $7.66 \text{ t ha}^{-1}$ ), now used as male parents, had the highest yields when in hybrid combination (Table 5). As for the Non-Stiff-Stalk populations, now used as female parents, highest average yields in hybrid combination were detected for BS11(FR)C14 ( $7.35 \text{ t ha}^{-1}$ ) and BS29(R)C3 ( $7.18 \text{ t ha}^{-1}$ ). The population BS29(R)C3 has only undergone three cycles of recurrent selection compared with the 14 cycles of reciprocal recurrent selection for BS11(FR)C14, but BS29(R)C3 shows a good response to combining well in crosses with other populations. Regarding the crosses *per se*, the average grain yield ranged from  $8.04 \text{ t ha}^{-1}$  for the cross BSCB1(R)C14 x BSSS(R)C14 to a low of  $5.42 \text{ t ha}^{-1}$  for BS16(S)C2 x BS34(S)C4; two populations that have undergone fewer cycles of recurrent selection. Again, the difference between the highest and lowest yielding crosses exceeded the  $\text{LSD}_{0.05}$  value suggesting significant differences existing among the population cross mean yields.

Contrasting grain yield population averages between the Design II crosses and the Reciprocal Design II crosses shows results that deviated from normal expectations (Table 4 and Table 5). In some cases, Stiff-Stalk populations when used as females (Design II crosses) showed decreased population hybrid combination averages compared with when the same population is used as a male (Reciprocal Design II crosses). Generally, Stiff-Stalk populations have been used more frequently as female parents because plants produce good ears. Troyer (2000) described Stiff-Stalk populations as possessing long, slightly tapered ears of medium maturity, well filled tips and butts, and have 16 to 22 closely spaced, dove-tailed kernel rows on small, dark red cobs with small shank attachments. Stiff-Stalk populations are also characterized by plants that have generally good stalk characteristics and tassels that are smaller and contain fewer tassel branches. The Non-Stiff-Stalk populations, as described by Troyer (2000), contained plants that have ears that are long, slender, 10 to 14 kernel rows, have greater kernel size, and larger diameter shanks. The plants are usually tall,

with medium high ear height and large, multi-branched tassels, which enable them to be used frequently as male parents to insure adequate pollen production. These plant characteristics allow the hybridization of a female Stiff-Stalk population with a male Non-Stiff-Stalk population to result in a high yielding cross superior to the reciprocal cross.

However, the placement of these populations into distinct heterotic groupings and patterns was determined on the basis of germplasm availability and experimental trials of inbred lines in crosses (Hallauer, 1997b). Therefore, the exact placement of a population into distinct heterotic group could have changed after trait selection and selection for the presence of favorable alleles emphasizing the particular traits from each respective population's particular recurrent selection program. Generally, the effects of reciprocal crosses between populations are not studied because Comstock and Robinson (1952) suggested that nongenetic maternal effects usually are assumed absent in maize populations. Therefore, since maternal and reciprocal effects are assumed to be absent or small in maize, reciprocal crosses usually are not grown (Hallauer and Martinson, 1975). However, Hallauer and Martinson (1975) detected significant maternal effects and some reciprocal effects for most agronomic traits when evaluating single crosses of normal maize cytoplasm and Texas-male sterile cytoplasm for fungal damages after being inoculated with the fungus *Bipolaris Maydis* (Nisikado) Shoemaker, race T.

In this study, differences among population averages derived in hybrid combinations between the Design II crosses and the Reciprocal Design II crosses were non-significant based on a  $LSD_{0.05}$  comparison. Significant differences among crosses *per se* were detected in a separate analysis evaluating only reciprocal mean differences between the crosses. The overall reciprocal effect was nonsignificant ( $Pr > 0.05$ ), but a few crosses showed significant reciprocal differences suggesting that grain yield was dependent on how the cross was produced (Table 9). The crosses BS11(FR)C14 x BS13(S)C9, BS16(S)C2 x BS13(S)C9, and BS28(R)C3 x BS11(FR)C14 showed significant reciprocal differences in grain yield. BS13(S)C9 had consistent negative estimates for all population crosses suggesting greater yields are obtained when BS13(S)C9 is used as a male, which is the opposite trend in the commercial seed industry.

Table 9. Mean difference† in grain yield between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses§		Stiff-Stalk (A)							Average
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
----- t ha <sup>-1</sup> -----									
BS11(FR)C14	(1)	0.24§	-0.60*	0.18	-0.43	-0.29	0.70*	-0.50	-0.10
BS26(S)C4	(1)	0.01	-0.12	-0.34	0.18	0.16	0.17	-0.20	-0.02
BSCB1(R)C14	(1)	0.19	-0.29	-0.17	0.41	-0.51	-0.03	0.39	0.00
BS16(S)C2	(2)	0.29	-0.56*	-0.19	0.05	-0.37	-0.07	0.32	-0.07
BS29(R)C3	(2)	0.14	-0.39	-0.50	-0.34	-0.01	0.11	0.00	-0.14
Average		0.17	-0.39	-0.20	-0.02	-0.20	0.18	0.00	-0.07

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 0.29.

Estimates of overall general combining ability (GCA) and specific combining ability (SCA) were calculated by averaging grain yield means across both designs for population crosses and populations *per se* (Table 10). The Stiff-Stalk populations BSSS(R)C14, BS13(S)C9, and BS10(FR)C14 had the largest, positive, highly significant GCA effects of 0.60, 0.53, and 0.50 t ha<sup>-1</sup>, respectively. These three populations also had relatively high average grain yields in hybrid combination between both groups of crosses. Echandi and Hallauer (1996) reported large positive highly significant GCA estimates for BSSS(R)C12 and BSCB1(R)C12 of 0.74 and 0.50 t ha<sup>-1</sup> in their diallel study. The BSCB1(R)C14 population in this study had a significantly positive GCA estimate of 0.16 t ha<sup>-1</sup> which is contradictory to the larger GCA estimate reported by Echandi and Hallauer (1996). BS34(S)C4 had the lowest GCA estimate reporting a significantly negative GCA value of -0.89 t ha<sup>-1</sup>. The negative GCA estimate of BS34(S)C4 corresponded directly with it having the lowest average grain yields achieved while in hybrid combination (Tables 4 and 5). BS29(R)C3 was the only adapted exotic population to have a positive significant GCA estimate of 0.15 t ha<sup>-1</sup>, suggesting adequate ability for the population to combine well on average with other populations. Positive GCA estimates are important, because they result from cumulative, additive gene effects that allow the population to perform well in multiple environments (Troyer, 2000).

The largest significant positive SCA estimate was 0.43 t ha<sup>-1</sup> for the cross of BS34(R)C3 x BS11(FR)C14 (Table 10); however, this cross achieved grain yields similar to the population cross averages reported among both designs. The cross BS10(FR)C14 x BS29(R)C3 had the second highest positive significant SCA effect of 0.35 t ha<sup>-1</sup>, with this cross also exhibiting the highest cross combination yield, implying that nonadditive dominance effects are present for producing a superior intervarietal cross. The cross BS28(R)C3 x BS29(R)C3 had the lowest SCA with a significant negative estimate of -0.45 t ha<sup>-1</sup>. Echandi and Hallauer (1996) reported a similar significantly negative SCA estimate of -0.46 t ha<sup>-1</sup> for the BS28 x BS29 cross before any recurrent selection program was initiated.

Stiff-Stalk and Non-Stiff-Stalk maternal GCA effects and reciprocal SCA effects were estimated by averaging the difference between the Design II crosses and Reciprocal Design II crosses. The combined data analysis showed a significant maternal GCA effect

Table 10. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for grain yield averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)† -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
		----- t ha <sup>-1</sup> -----							
BS11(FR)C14	(1)	-0.24*§	-0.13	-0.02	0.20	-0.36**	0.11	0.43**	0.33**¶
BS26(S)C4	(1)	0.05	0.15	-0.01	-0.29**	0.14	0.18	-0.23*	-0.27**
BSCB1(R)C14	(1)	-0.12	0.06	0.06	-0.17	0.06	0.20	-0.09	0.16**
BS16(S)C2	(2)	-0.05	-0.06	0.10	0.21	-0.04	-0.04	-0.12	-0.38*
BS29(R)C3	(2)	0.35**	-0.02	-0.13	0.04	0.20	-0.45**	0.00	0.15**
Stiff-Stalk GCA		0.50**#	0.53**	-0.14*	-0.22**	0.60**	-0.38**	-0.89**	0.00

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.12.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.05.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.06.

among the Stiff-Stalk populations only. The population BS13(S)C9 showed a highly significant maternal GCA effect of  $-0.32 \text{ t ha}^{-1}$  (Table 11). This population showed a decrease of  $0.32 \text{ t ha}^{-1}$  on average when crossed with other populations as the female parent in crosses verses being used as a male parent in crosses. BS10(FR)C14 and BS28(R)C3 had positive significant maternal GCA estimates of  $0.24 \text{ t ha}^{-1}$ . The reciprocal mean square in the combined data analysis was nonsignificant, but two crosses, both involving the Non-Stiff-Stalk parent BS11(FR)C14, showed significant differences from zero for grain yield (Table 11). The cross, BS28(R)C3 x BS11(FR)C14, showed a  $0.55 \text{ t ha}^{-1}$  increase in grain yield when BS28(R)C3 was used as the female parent in the cross and the cross, BS34(S)C4 x BS11(FR)C14 showed a decrease of  $-0.47 \text{ t ha}^{-1}$ , when BS34(R)C4 was used as the female parent in the cross.

A calculation of heterosis or hybrid vigor is also important in determining the superiority of a hybrid over its parents. Two estimates of heterosis, mid-parent heterosis and percentage mid-parent heterosis, were calculated and are reported in Table 12 for Design II crosses and Table 13 for Reciprocal Design II crosses. Mid-parent heterosis is expressed as the difference between the  $F_1$  cross and the mid-parent value and was used to determine if the level of mid-parent heterosis expressed by the cross is significantly different from zero. Percentage mid-parent heterosis was calculated by taking the mid-parent heterosis value and dividing it by the mid-parent value. Both values will be presented simultaneously for each cross and presented as an average for each particular population.

Mid-parent heterosis values for the Design II crosses ranged from a low of  $0.96 \text{ t ha}^{-1}$  or 18 % for the cross BS28(R)C3 x BS29(R)C3 to a high of  $3.16 \text{ t ha}^{-1}$  or 72% for the cross BSCB1(R)C14 x BSSS(R)C14 (Table 12). Average percentage mid-parent heterosis among all Design II crosses was 34.7% (Table 6). As for the Reciprocal Design II crosses, mid-parent heterosis and percentage mid-parent heterosis ranged from a low of  $0.97 \text{ t ha}^{-1}$  or 16% for BS16(S)C2 x BS10(FR)C14 to a high of  $3.67 \text{ t ha}^{-1}$  or 84% for the cross BSCB1(R)C14 x BSSS(R)C14 (Table 13). Average percentage mid-parent heterosis expressed among all Reciprocal Design II crosses was 35.9% (Table 6). All mid-parent heterosis estimates were significantly different from zero for all crosses in both designs. The cross BSSS(R)C14 x BSCB1(R)C14 exhibited the highest mid-parent heterosis and percent mid-parent heterosis



Table 11. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for grain yield calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
		----- t ha <sup>-1</sup> -----							
BS11(FR)C14	(1)	0.10§	-0.17	0.41	-0.37	-0.06	0.55*	-0.47*	-0.03¶
BS26(S)C4	(1)	-0.21	0.22	-0.18	0.16	0.31	-0.05	-0.25	0.05
BSCB1(R)C14	(1)	-0.05	0.04	-0.03	0.37	-0.37	-0.27	0.32	0.07
BS16(S)C2	(2)	0.13	-0.16	0.03	0.08	-0.16	-0.24	0.32	-0.01
BS29(R)C3	(2)	0.04	0.07	-0.23	-0.24	0.27	0.01	0.07	-0.07
Stiff-Stalk GCA		0.24*#	-0.32**	-0.14	0.04	-0.14	0.24*	0.07	0.00

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.24.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.10.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.12.

Table 12. Grain yield mid-parent heterosis, expressed as the difference in t ha<sup>-1</sup> between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

(A-22) Populations Compared Across Populations																	
Populations		SS Females (A)‡															
		----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -					
		NSS Males (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4	
		t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%
BS11(FR)C14	(1)	1.38**	22	1.86**	33	1.66**	30	1.56**	28	2.05**	38	1.99**	37	1.62**	33	1.73**	32
BS26(S)C4	(1)	1.28**	21	2.11**	40	1.14**	22	1.09**	21	2.50**	50	1.52**	30	0.84**	18	1.50**	29
BSCB1(R)C14	(1)	2.28**	43	3.01**	66	2.36**	51	2.40**	53	3.16**	72	2.51**	57	2.35**	59	2.58**	57
BS16(S)C2	(2)	1.26**	21	1.62**	31	1.27**	24	1.48**	29	2.00**	40	1.12**	22	1.15**	25	1.41**	28
BS29(R)C3	(2)	1.75**	28	1.90**	34	1.04**	19	1.27**	23	2.58**	48	0.96**	18	1.28**	26	1.54**	28
Average		1.59**	27	2.10**	41	1.49**	29	1.56**	31	2.46**	50	1.62**	33	1.45**	32	1.75**	35

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 0.25.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table 13. Grain yield mid-parent heterosis, expressed as the difference in  $t\ ha^{-1}$  between the  $F_1$  cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal  $F_1$  Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Females (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average
		t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%	t ha <sup>-1</sup>	%
BS11(FR)C14	(1)	1.14**	18	2.46**	44	1.48**	26	1.98**	36	2.34**	44	1.29**	24	2.12**	43	1.83**	34
BS26(S)C4	(1)	1.28**	21	2.23**	43	1.47**	28	0.91**	18	2.34**	47	1.35**	27	1.04**	22	1.52**	29
BSCB1(R)C14	(1)	2.09**	39	3.29**	72	2.53**	55	1.99**	44	3.67**	84	2.54**	57	1.96**	49	2.58**	57
BS16(S)C2	(2)	0.97**	16	2.18**	42	1.46**	28	1.43**	28	2.37**	48	1.19**	24	0.83**	18	1.49**	29
BS29(R)C3	(2)	1.61**	26	2.29**	41	1.54**	28	1.60**	29	2.59**	49	0.85**	16	1.27**	26	1.68**	31
Average		1.42**	24	2.49**	49	1.69**	33	1.58**	31	2.66**	54	1.44**	29	1.44**	32	1.82**	36

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 0.25.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

BS28(R)C3 x BS29(R)C3 (Table 12 and Table 13). Lower percentage mid-parent heterosis estimate for the BS28 x BS29 cross also was reported by Echandi and Hallauer (1996).

Mid-parent heterosis and percentage mid-parent heterosis estimates between U.S. Corn Belt material and adapted exotic material were significantly different from zero for grain yield. The adapted tropical populations, BS28(R)C3 and BS34(S)C4, showed the highest mid-parent heterosis estimates when crossed with the U.S. Corn Belt population BSCB1(R)C14 (Table 12 and Table 13). Similar to BSCB1(R)C14, the other U.S. Corn Belt population BSSS(R)C14 showed high mid-parent heterosis estimates when crossed with the adapted exotic populations BS16(S)C2 and BS29(R)C3.

Stability among heterotic patterns between Stiff-Stalk populations and Non-Stiff-Stalk populations was illustrated in this experiment. Design II crosses and Reciprocal Design II crosses confirmed that the Reid Yellow Dent populations (Stiff-Stalk germplasm), BS10(FR)C14 and BSSS(R)C14, and the Lancaster Sure Crop populations (Non-Stiff-Stalk germplasm), BS11(FR)C14 and BSCB1(R)C14, had the highest average grain yield, average percentage mid-parent heterosis estimates, and overall general combining ability estimates compared with the other populations in the study. These populations when placed in cross combinations between them, resulted in crosses that had higher yields, higher mid-parent and percentage mid-parent heterosis estimates, and on average larger positive SCA estimates.

Agronomic phenotypic data also suggest that the following heterotic combinations should be investigated further: the Design II cross of the Reid Yellow Dent population BS10(FR)C14 x adapted exotic population BS29(R)C3 (Suwan-1) and the Reid Yellow Dent population BSSS(R)C14 x BS29(R)C3 with crosses yielding  $8.03 \text{ t ha}^{-1}$  and  $7.91 \text{ t ha}^{-1}$ , respectively. The cross BSSS(R)C14 x BS29(R)C3 had a percentage mid-parent heterosis estimate of 48% which agreed with the percentage mid-parent heterosis estimate of 52.9% reported by Echandi and Hallauer (1996) for the cross. A significantly positive, SCA estimate of  $0.35 \text{ t ha}^{-1}$  was estimated for the cross BS10(FR)C14 x BS29(R)C3. The adapted tropical heterotic pattern BS28(R)C3 x BS29(R)C3, or Tuxpeño x Suwan-1, was not confirmed with the cross having a significantly negative SCA estimate of  $-0.44 \text{ t ha}^{-1}$  and the lowest Design II cross mid-parent heterosis and percentage mid-parent heterosis estimates of  $0.96 \text{ t ha}^{-1}$  and 18%, respectively.

Population placement into Stiff-Stalk and Non-Stiff-Stalk categories was also explored by inclusion of reciprocal crosses for identification of maternal and reciprocal effects. A highly significant maternal effect for grain yield was detected for the Stiff-Stalk population BS13(S)C9 of  $-0.32 \text{ t ha}^{-1}$ . This GCA estimate suggests that a  $0.32 \text{ t ha}^{-1}$  reduction in grain yield occurred when the population was used as a female verses its use as a male parent. Although lines derived from the BS13(S)C9 population have been used as females to produce hybrid seed, the estimate for maternal effect ( $-0.32 \text{ t ha}^{-1}$ ) suggests greater yields are possible if used as male parent to produce hybrid seed.

### **Grain Moisture**

Grain moisture means for the 35 Design II (A x B) crosses, the 35 Reciprocal Design II (B x A) crosses and the 12 parent populations *per se* calculated across six environments are presented in Table A1 and Table A2, respectively. A relatively low grain moisture mean indicates fast dry down and is usually desired for a reduction in grain storage and handling problems. Grain moisture means for the 12 Stiff-Stalk and Non-Stiff-Stalk populations will be discussed in detail.

Grain moisture means for the Stiff-Stalk populations *per se* ranged from a low of 18.8% for BS13(S)C9 to a high of 23.4% for BS34(S)C4, whereas the Non-Stiff-Stalk populations *per se* grain moisture means ranged from a low of 18.1% for BS11(FR)C14 to a high of 22.0% for the population BS29(R)C3 (Table A1). Significant differences between parent population grain moisture means were indicated by the difference between high and low grain moisture means exceeding the parent  $\text{LSD}_{0.05}$  of 0.6%. The average grain moisture means for the Stiff-Stalk and Non-Stiff-Stalk populations both 19.8% were not significantly different based on the  $\text{LSD}_{0.05}$  (Table 6). The two highest grain moisture populations were BS34(S)C4 and BS29(R)C3 (23.4% and 22.0%, respectively) indicating the major weakness of exotic materials as described by Goodman (1985) of high moisture and slow dry down of kernels (Table A1). However, the adapted exotic population, BS28(R)C3 exhibited a grain moisture of 18.9%, which is statistically similar to U.S. Corn Belt populations BS10(FR)C14 and BSSS(R)C14, indicating that six cycles of mass selection for adaptation and three cycles of recurrent selection were effective in decreasing grain moisture percentage. The lowest two parent population grain moisture means were exhibited by the populations BS11(FR)C14

(18.1%) and BSCB1(R)C14 (18.4%) following 14 cycles of reciprocal recurrent selection. Echandi and Hallauer (1996) reported a similar trend with the two populations having the lowest grain moistures in their diallel study.

The Stiff-Stalk Cycle 0 population BS10C0 had the lowest parent grain moisture of 18.6% compared with the Stiff-Stalk population BSKC0 that had the highest grain moisture of 19.3% (Table 7). Among the Non-Stiff-Stalk populations grain moisture means ranged from a low of 18.1% for BSCB1C0 to a high of 21.6% for BS11C0. Highly significant differences were detected only among the Non-Stiff-Stalk Cycle 0 populations. The average grain moisture among all Cycle 0 populations was 19.4% (Table 6).

Population improvement over successive cycles of recurrent selection was evaluated for the grain moisture trait by comparison of Stiff-Stalk and Non-Stiff-Stalk U.S. Corn Belt Cycle *I* and Cycle 0 populations. All populations showed a positive increase in percent grain moisture except the population BS11 (Table 8). Following 14 cycles of reciprocal recurrent selection, BS11(FR)C14 showed a highly significant reduction in percent grain moisture of -3.5% compared with the BS11C0 population. The population BSK(HI)C11 showed a highly significant increase in grain moisture of 0.7%. Tanner (1984) reported a similar finding for BSK(HI) in which a significant 1.3 % increase in grain moisture occurred between the Cycle 0 and Cycle 8 BSK(HI) populations *per se*.

Population crosses *per se* had a average grain moisture of 19.8% compared with the parents average grain moisture of 19.8% (Table 6). The difference in grain moisture between parents and crosses was nonsignificant and no average heterosis was expressed in terms of grain moisture. The Design II crosses had a average grain moisture of 19.8%, while the Reciprocal Design II crosses had an average grain moisture of 19.8%. The difference in grain moisture partitioned between the two styles of crosses was nonsignificant based on the  $LSD_{0.05}$ .

Among Design II crosses grain moisture means ranged from a high of 21.9% for the cross BS34(S)C4 x BS26(S)C4 to a low of 18.2% for the cross BSSS(R)C14 x BS11(FR)C14 (Table A1). Significant differences among crosses were detected based on the  $LSD_{0.05}$ . The Design II crosses BSSS(R)C14 x BS11(FR)C14 and BS10(FR)C14 x BSCB1(R)C14 had grain moistures that were within one  $LSD_{0.05}$  higher, but not significantly different from, the

LH198 x LH185 hybrid check grain moisture of 17.8%. On average, crosses including the population BS11(FR)C14 had the lowest grain moistures in hybrid combination of 18.9%. The adapted exotic population BS34(S)C4 had the highest grain moisture in hybrid combination of 21.3%. This observation clarifies Goodman's (1985) statement that adapted exotic populations still maintain deleterious alleles contributing to higher grain moisture in both population *per se* and in cross performance. Interestingly, the adapted exotic population BS28(R)C3 had the lowest grain moisture among adapted exotic materials and was significantly lower than the U.S. Corn Belt populations BSK(HI)C11 and BS26(S)C4.

Among the Reciprocal Design II crosses, grain moisture means ranged from a high of 22.4% for the cross BS29(R)C3 x BS34(S)C4 to a low of 18.0% for the cross BS11(FR)C14 x BS13(S)C9 (Table A2). The low grain moisture of the BS11(FR)C14 x BS13(S)C9 cross was not significantly different compared with the 17.8% grain moisture of the hybrid check LH198 x LH185. The nonadditive effects expressed by the BS11(FR)C14 x BS13(S)C9 cross suggests recurrent selection has been successful in removing deleterious alleles causing higher grain moisture in both populations. The highest grain moisture was found in a cross between two adapted tropical populations implying future continuation for selection for lower grain moisture is necessary. On average crosses having BS11(FR)C14 as one of the parents when in hybrid combination had the lowest average grain moisture of 18.9% (Table A2). The average grain moisture of BS11(FR)C14 was less, but not statistically significant, compared with the Design II crosses BS11(FR)C14 average grain moisture. BS34(S)C4 had the highest average grain moisture when in hybrid combination of 21.3%. Again, this Reciprocal Design II BS11(FR)C14 population average was less, but not significantly less, than the Design II BS11(FR)C14 population average.

Differentiating between Design II and Reciprocal Design II population averages shows some Reciprocal Design II populations and crosses *per se* having lower grain moisture mean percentages than the Design II population averages and crosses *per se*. The reciprocal effect is also evident in the agronomic phenotypic data. Contrasting grain moisture population averages in hybrid combination with the  $LSD_{0.05}$  shows no significant differences existing between population averages. However, for the crosses *per se*, a second separate analysis was conducted to examine reciprocal mean differences existing among Design II and

values in both the Design II and Reciprocal Design II crosses (Table 12 and Table 13). Echandi and Hallauer (1996) and Keeratinjakal and Lamkey (1993) had similarly large estimates of mid-parent heterosis of 76.8% and 76.0%, which agree with this studies estimates of percentage mid-parent heterosis. However, these large mid-parent heterosis estimates (72.0 and 84.0%) are over inflated because the BSCB1(R)C14 population had the lowest parent mean among the 12 parents (Table 4). On average, crosses that had the greatest mid-parent heterosis in both Design II and Reciprocal Design II crosses occurred when BSCB1(R)C14 was used as one of the parents in the crosses. This trend with crosses showing the greatest heterotic response with the population BSCB1(R)C14 was also reported by Echandi and Hallauer (1996). This suggests that the reciprocal recurrent selection program initiated within the BSCB1(R)C14 population has been successful with increasing the number and frequency of favorable alleles present within the existing BSCB1(R)C14 population when used in crosses.

The population BS10(FR)C14, however, had on average the lowest mid-parent heterosis estimates in both the Design II crosses and the Reciprocal Design II crosses. The occurrence of these low mid-parent heterosis values could be due to the BS10(FR)C14 population having the highest parent grain yield mean among the 12 parents (Table 4). All crosses including the population BS10(FR)C14 had mid-parent heterosis values significantly different from zero ( $Pr < 0.01$ ). The Design II cross BS10(FR)C14 x BS11(FR)C14 and the Reciprocal Design II cross of BS11(FR)C14 x BS10(FR)C14 had mid-parent heterosis values and percent mid-parent heterosis values of 1.38 t ha<sup>-1</sup> and 22% and 1.14 t ha<sup>-1</sup> and 18%, respectively. These smaller percentage mid-parent heterosis results contradict the 39.7% percent mid-parent heterosis estimated by Eyherabide and Hallauer (1991) in the cross BS10(FR)C8 x BS11(FR)C8.

Mid-parent heterosis values among adapted exotic crosses were the highest in both the Design II crosses and the Reciprocal Design II crosses for the cross of BS34(S)C4 x BS29(R)C3. However, the well-known and well-documented adapted tropical heterotic pattern of Suwan-1 (BS29) and Tuxpeño (BS28) (Goodman, 1985) was not documented in this experiment. The lowest estimates of mid-parent heterosis and percentage mid-parent heterosis were reported for both the Design II cross and the Reciprocal Design II cross of



Reciprocal Design II crosses for grain moisture. Three crosses had significantly different reciprocal effects from zero at the five percent significance level (Table B1). The cross BSK(S)C11 x BS11(FR)C14 had a 0.6% higher grain moisture in the Design II cross versus the Reciprocal Design II cross. The other two crosses, BSK(HI)C11 x BS26(S)C4 and BS34(S)C4 x BS29(R)C3, had 0.6 and 0.6% lower grain moistures, respectfully, in the Design II crosses versus the Reciprocal Design II crosses.

Overall, grain moisture GCA and SCA estimates were calculated based on the cross and population average means of both designs (Table C1). For grain moisture, negative GCA and SCA estimates indicate reduced grain moisture and should aid the crosses in overall agronomic performance. For the Stiff-Stalk populations, BS10(FR)C14 had the largest highly significant negative GCA estimate of -0.6% and correlates with the population having the lowest average grain moisture in hybrid combination in both Design II and Reciprocal Design II crosses. Among Non-Stiff-Stalk populations BS11(FR)C14 had the largest highly significant negative GCA estimate of -0.9% and also resulted in the lowest grain moisture population average when in hybrid combination. These estimates imply that both the BS10(FR)C14 and BS11(FR)C14 population have favorable alleles present that result in decreased grain moisture in cross performance. A highly significant GCA estimate for BS11(FR)C14 was also observed by Echandi and Hallauer (1996). The adapted exotic populations BS34(S)C4 and BS29(R)C3 had highly significant positive GCA estimates of 1.4% and 1.1% indicating higher grain moisture percentages in crosses involving these populations. The BS28(R)C3 population was the only population among the four exotics that had a significantly negative GCA of -0.2%, indicating a good potential for this population to be used in crosses in the future.

Overall SCA estimates ranged from -0.4% for BS34(S)C4 x BS16(S)C2 to a SCA estimate of 0.4 for BSK(HI)C11 x BS16(S)C2 (Table C1); both SCA values were significantly different from zero at the one percent significance level. Despite the cross BS34(S)C4 x BS16(S)C2 having the largest negative SCA estimate (-0.4%), the cross displayed a higher grain moisture among all Design II and Reciprocal Design II crosses. The cross BS11(FR)C14 x BS10(FR)C14, having the two populations with the highest negative

GCA estimates, however, had a significantly positive SCA estimate of 0.2% suggesting dominance effects within the intervarietal cross led to a higher percent grain moisture.

The statistical contrasts used to calculate Stiff-Stalk and Non-Stiff-Stalk GCA maternal effects and the Reciprocal SCA effects (interaction between Stiff-Stalk and Non-Stiff-Stalk maternal effects) for the combined analysis all showed non-significance ( $Pr > 0.05$ ) for grain moisture. However, estimate statements used to calculate maternal GCA and reciprocal SCA estimates did identify a Stiff-Stalk maternal GCA estimate and reciprocal SCA estimates significantly different from zero. The BSK(S)C11 Stiff-Stalk population showed a significantly positive GCA estimate of 0.2% suggesting that the BSK(S)C11 population results in a higher moisture cross when used as a female parent verses being used as a male parent (Table D1). The cross BSSS(R)C14 x BS26(S)C4 showed a highly significantly positive reciprocal SCA estimate of 0.6%, suggesting a higher moisture cross when BSSS(R)C14 is used as a female compared with being used as a male parent in the cross. Similarly, both BS10(FR)C14 x BSCB1(R)C14 and BS34(S)C4 x BS29(R)C3 had highly significant negative reciprocal SCA estimates of -0.5%, indicating a lower moisture cross when BS10(FR)C14 and BS34(S)C4 are used as female parents in the above crosses compared with the reciprocal cross. Detection of grain moisture maternal and reciprocal effects were also reported by Hallauer and Martinson (1975) in their study examining normal cytoplasm and Texas male-sterile cytoplasm single crosses for tolerance to fungus infection.

Mid-parent heterosis calculations provided estimates of heterosis for grain moisture among the Design II and Reciprocal Design II crosses in the study. Average percent mid-parent heterosis for grain moisture among Design II crosses was a positive 0.1% compared to the Reciprocal Design II crosses positive average grain moisture percent mid-parent heterosis of 0.1% (Table 6). The average difference in grain moisture among population crosses was nonsignificant ( $Pr > 0.05$ ). Negative values of mid-parent heterosis and percent mid-parent heterosis are desired since negative values indicate reduced grain moisture in the cross compared with the parental average.

Among Design II crosses, grain moisture mid-parent heterosis and percent mid-parent heterosis values ranged from negative highly significant values of -0.8% and -4% for the cross BS34(S)C4 x BS29(R)C3 to positive significant values of 0.6% and 3% for the cross

BSK(HI)C11 x BS16(S)C2 (Table E1). The former cross with the highest negative mid-parent heterosis values, however, had the two highest grain moisture parents used in the study (Table A1). Among U.S. Corn Belt Crosses, BS10(FR)C14 x BSCB1(R)C14 and BSSS(R)C14 x BS11(FR)C14 showed the greatest negative percent mid-parent heterosis estimates of -2%. Percent mid-parent heterosis estimates deviated among crosses either higher or lower compared with the percent mid-parent heterosis estimates calculated by Echandi and Hallauer (1996) and Michelini and Hallauer (1993). The deviation among crosses, however, could be caused by higher or lower parental grain moisture means for each independent study.

Among Reciprocal Design II crosses, grain moisture mid-parent heterosis and percent mid-parent heterosis estimates ranged from a highly significant negative values of -1.0% and -5% for the cross BS16(S)C2 x BS34(S)C4 to highly significantly positive values of 0.7% and 4% for the cross BS26(S)C4 x BS28(R)C3 (Table E2). The cross BS29(R)C3 x BS10(FR)C14 had significantly negative mid-parent heterosis and percent mid-parent heterosis estimates of -0.6% and -3%, which parallels the 19.9% grain moisture mean for the cross *per se* and is statistically similar to the average grain moisture mean of 19.8% for all Reciprocal Design II crosses (Table A2). Grain moisture percent mid-parent heterosis values among Reciprocal Design II crosses either increased or decreased on average 1 to 2% compared with their Design II counterpart crosses.

Expression of heterosis among heterotic groups and in heterotic patterns was primarily evident for grain moisture through the overall GCA and SCA estimates described earlier (Table C1). Echandi and Hallauer (1996) also suggested that grain moisture heterosis was primarily evident in their calculated GCA estimates. Percent mid-parent heterosis estimates for most crosses showed relatively little or no heterotic improvement compared with the parental average. However, overall GCA effects showed that most populations advanced through 10 or more cycles of recurrent selection had negative GCA estimates indicating reduced grain moisture when that parent population is used in crosses. In some instances, population crosses showed significantly negative SCA estimates, but the cross usually had a grain moisture mean higher than either the Design II or Reciprocal Design II cross average. Based on SCA values, the heterotic cross combinations BS10(FR)C14 x

BSCB1(R)C14 and BSSS(R)C14 x BS11(FR)C14 (both Reid Yellow Dent x Lancaster Sure Crop crosses) should continue to be investigated for reduced grain moisture crosses and selected within for inbred lines in future studies. Overall, SCA estimates showed heterotic patterns being maintained among all Design II and Reciprocal Design II crosses.

### **Root and Stalk Lodging**

Root and stalk lodging means for the 35 Design II population crosses between Stiff-Stalk and Non-Stiff-Stalk populations and the 12 parent populations *per se* are presented in Table A3 and Table A5. Reciprocal Design II population crosses along with the 12 population *per se* root and stalk lodging means are presented in Table A4 and Table A6. Relatively small root and stalk lodging means amongst population crosses and populations *per se* are usually desired by plant breeders since both agronomic traits have a negative impact on potential crop performance (*i.e.*, grain yield). Population crosses and populations *per se* with low root and stalk lodging means are represented as having good root and stalk characteristics and are generally selected for and selected among in most plant breeding programs. Root and stalk lodging means for the 12 parent populations used in this study will be discussed in detail.

Root lodging means for the seven Stiff-Stalk populations ranged from a low of 5.8% for BS13(S)C9 to a high of 47.1% for BS34(S)C4, while Non-Stiff-Stalk populations root lodging means ranged from a low of 17.9% for BS26(S)C4 to a high of 32.8% for BS29(R)C3 (Table A3). Stalk lodging means for the Stiff-Stalk populations ranged from a low of 5.1% for BS34(S)C4 to a high of 19.6% for BSK(S)C11, while stalk lodging means for Non-Stiff-Stalk populations ranged from a low of 4.8% for BSCB1(R)C4 to a high of 14.0% for BS26(S)C4 (Table A5). The average percent root and stalk lodging means for Stiff-Stalk and Non-Stiff-Stalk parents was 23.8% and 9.2%, respectively (Table 6).

Root lodging means for all populations except BS34(S)C4 used in the study were not statistically different from the root lodging mean of the hybrid check LH198 x LH185 of 16.9% based on a  $LSD_{0.05}$  of 15.1%. The populations BS13(S)C9 and BSSS(R)C14, both derived from BSSS, had the two lowest root lodging values (5.8% and 16.3%) and two of the lowest stalk lodging values (5.3% and 5.9%) among the 12 populations (Table A3). BSSS was developed as a population for good root and stalk quality and these results offer

confirmation to the aforementioned reasoning. Low root and stalk lodging means for BSSS have also been confirmed by Mungoma and Pollack (1988), Michelini and Hallauer (1993), and Echandi and Hallauer (1996). The population BSCB1(R)C14 had the lowest stalk lodging mean of 4.8% implying that reciprocal recurrent selection has indirectly selected for favorable alleles accenting high stalk quality within the BSCB1(R)C14 (Table A5). An adapted exotic population BS28(R)C3 had the lowest mean stalk lodging (6.7%) among the four exotic populations suggesting a potential population for providing genetic diversity in future maize crosses for stalk lodging resistance.

U.S. Corn Belt Cycle 0 population root lodging means ranged from a low of 24.1% for BS10C0 to a high of 46.0% for BSKC0 (Table 7); both populations are classified within the Stiff-Stalk group. While stalk lodging means amongst the U.S. Corn Belt populations ranged from a low of 12.7% for the population BS26C0 (Non-Stiff-Stalk) to a high of 19.8% for the BSCB1C0 population (Table 7). The high and low stalk lodging means among the populations were among the Non-Stiff-Stalk populations. Significant differences for root lodging were only detected among the Stiff-Stalk populations, while no significant differences among the populations were detected for stalk lodging based on the  $LSD_{0.05}$ . Root lodging and stalk lodging Cycle 0 population averages were 18.9% and 6.5% respectively.

Population performance after '*I*' cycles of recurrent selection was evaluated in a separate analysis comparing root lodging and stalk lodging means among the Cycle *I* and Cycle 0 U.S. Corn Belt populations. A negative percentage value should be anticipated indicating a reduction in root lodging and stalk lodging with selection from the Cycle 0 to the Cycle *I* populations. The Stiff-Stalk population BS13(S)C9 showed a highly significant reduction of -25.6% for root lodging after nine cycles of recurrent selection (Table 8). BSK(S)C11 and BSK(HI)C11, both Stiff-Stalk populations, were the only other two populations that showed significant reductions in root lodging of -24.2% and -15.7%, respectively. Tanner and Smith (1987) indicated a reduction in root lodging of -23% for BSK(S)C8 and -8.6% for BSK(HI)C8 after eight cycles of  $S_1$ (S) and half-sib (HI) recurrent selection, respectively. Significant reductions in stalk lodging were only detected for BSCB1(R)C14 (-15.0%) and BS10(FR)C14 (-10.7%) populations, while no significant

differences for stalk lodging were detected among the other populations. Eyherabide and Hallauer (1991) showed a -4.6% reduction in the Stiff-Stalk population BS10 following eight cycles of full-sib reciprocal recurrent selection.

The 70 population crosses had an average percentage root lodging of 25.3% showing a 6.1% increase in root lodging compared with the parent mean of 23.8% (Table 6). Average percentage stalk lodging of the 70 population crosses was 8.2% which decreased 11.3% compared with the parent mean of 9.2% (Table 6). The differences in root lodging and stalk lodging between the population crosses and the parents were both nonsignificant ( $P > 0.05$ ) indicating that no expression of average heterosis occurred for either trait in this study (Table 3). Failure to observe an estimate of average heterosis was also reported by Echandi and Hallauer (1994), which believed that large differences between the adapted tropical and U.S. Corn Belt cultivars masked the potential for an average heterotic response for the two traits to be manifested.

Design II population cross root lodging and stalk lodging means are presented in Table A3 and Table A5. BS13(R)C9 x BS26(S)C4 had the lowest percent root lodging among the crosses of 16.2% followed by the cross BSSS(R)C14 x BS26(S)C4 with a root lodging mean of 17.0%. Overall, crosses that included BSSS(R)C14 and its related population BS13(S)C9 had the two lowest root lodging estimates when in hybrid combination. Echandi and Hallauer (1996) observed a similar trend in which crosses that included BSSS(R)C14 showed lower levels of root lodging on average. The Design II cross BS34(S)C4 x BS11(FR)C14 had the highest percent root lodging of 37.1%. Coincidentally, crosses that included BS34(S)C4 (32.1%), BS11(FR)C14 (27.1%), along with BS29(R)C3 (27.2%) had greater amounts of root lodging when in hybrid combination. BS34(S)C4 and BS29(R)C3 are both exotic populations illustrating Goodman's (1985) statement that exotic material has poor root characteristics when it is in temperate areas. Considering stalk lodging, the Design II cross BS28(R)C3 x BS16(S)C2, an all exotic germplasm cross, had the lowest percent stalk lodging of 3.5% followed by BS28(R)C3 x BSCB1(R)C14 (a 50% exotic cross) with 4.4% (Table A5). Low levels of stalk lodging were observed when the cross included the BS28(R)C3 (5.3%) population. The BS28(R)C3 population contains favorable alleles for increased stalk quality thus reducing stalk lodging within the population.

The BSCB1(R)C14 population also showed low levels of stalk lodging on average when in hybrid combination with a population average of 6.4%.

Reciprocal Design II population cross root lodging and stalk lodging means are presented in Table A4 and Table A6. Root lodging means ranged from a low of 9.5% for BS26(S)C4 x BS13(S)C9 to a high of 37.5% for the cross BS11(FR)C14 x BS34(S)C4. Similar to the Design II crosses, the reciprocal cross BS26(S)C4 x BS13(S)C9 (Design II cross 16.2% and Reciprocal Design II cross 9.5%) also had the lowest percent root lodging among the reciprocal crosses. Low levels of root lodging were seen among crosses that contained the populations BS13(S)C9 (17.5%), BSSS(R)C14 (19.3%), and BS26(S)C4 (21.2%) when in hybrid combination. The reciprocal cross BSCB1(R)C14 x BSSS(R)C14 with a mean percent root lodging of 16.5% was 0.4% lower in percent root lodging, but not statistically different from, the check LH198 x LH185 root lodging percentage of 16.9%. Reciprocal Design II stalk lodging values ranged from a low of 3.5% for BSCB1(R)C14 x BS28(R)C3 to a high of 17.2% for BS26(S)C4 x BSK(S)C11 (Table A6). Overall Reciprocal Design II population crosses stalk lodging average was 8.2% (Table 6). Exotic germplasm contributed favorable alleles for good agronomic stalk quality characteristics as the cross with the lowest stalk lodging percentage contained the adapted exotic population BS28(R)C3 or Tuxpeño germplasm. Population crosses containing BS28(R)C3 and BSCB1(R)C14 also had the lowest percent stalk lodging values of 5.5% and 6.2% when in hybrid combination. However, the highest levels of stalk-lodging were seen in crosses containing the U.S. Corn Belt population BSK(HI)C11 which had 13.1% stalk lodging on average when in hybrid combination.

Reciprocal Design II population cross root lodging and stalk lodging means and population *per se* averages were occasionally lower or higher when compared to the Design II population cross root lodging and stalk lodging means. Significant differences between population averages and population crosses were evaluated through contrasts in a separate analysis considering the difference between these two cross types (a reciprocal mean difference). The overall contrasts showed no significant differences ( $Pr > 0.05$ ) existing for either root lodging or stalk lodging for the crosses and the population averages. However, estimate statements indicated a significant difference in root lodging for the cross

BSK(S)C11 x BS29(R)C3 of -10.3% (Table B2). This estimate implied that the Reciprocal Design II cross BS29(R)C3 x BSK(S)C11 was 10.3% higher in root lodging compared with the Design II cross BSK(S)C11 x BS29(R)C3. Results indicated two significant differences existed among the stalk lodging estimates for BSK(S)C11 x BSCB1(R)C14 (-4.5%) and BS34(S)C4 x BS16(S)C2 (-5.7%) (Table B3). Negative values indicated higher levels of stalk lodging occurring for the Reciprocal Design II cross versus the Design II cross.

Overall estimates of GCA and SCA were calculated across the 70 population crosses for the traits root lodging and stalk lodging (Table C2 and Table C3). Similar to population cross means, negative GCA and SCA values are desirable since these estimates indicate a reduction in lodging compared with the population overall performance in crosses (GCA value) and for the specific cross *per se* in relation to parent population averages (SCA values). The populations BS13(S)C9 (-6.0%) and BSSS(R)C14 (-5.7%) had significantly negative GCA estimates, and correspondingly both populations had the lowest percentage root lodging population averages in hybrid combination (Table A3 and Table A4). The adapted exotic populations, BS34(S)C4, BS28(R)C3, and BS29(R)C3, also had significantly positive GCA estimates of 6.6, 2.4, and 2.1%, respectively, indicating that unfavorable alleles leading to poorer root qualities affected the additive nature of these populations (Table C2). A significantly negative estimate of GCA for BSSS(R)C14 (-1.9%) and significantly positive GCA estimates for BS27 (1.6%) and BS29 (2.0%) were also identified by Echandi and Hallauer (1996). A significantly negative root lodging SCA estimate of -5.1% was calculated for the cross BSK(HI)C11 x BS16(S)C2, despite BSK(HI)C11 (5.0%) having a significantly positive GCA estimate. Whereas the cross BS28(R)C3 x BS16(S)C2 had a significantly positive SCA estimate of 4.3% when the BS16(S)C2 (-1.9%) population had a significantly negative GCA estimate. These findings suggest that favorable alleles in the BS16(S)C2 population masked the deleterious alleles leading to increased root lodging in the cross BSK(HI)C11 x BS16(S)C2, but BS16(S)C2 failed to contribute favorable alleles for decreased root lodging when crossed with the adapted exotic population BS28(R)C3.

Highly significantly negative GCA estimates for stalk lodging were obtained for the populations BS28(R)C3 (adapted exotic population) and BSCB1(R)C14 (U.S Corn Belt population) of -2.8 and -1.9%, respectively (Table C3). Significantly negative GCA



estimates were also detected for the populations BSSS(R)C14 (-1.2%) and BS10(FR)C14 (-1.0%). The first three populations mentioned [BS28(R)C3 (5.3%); BSCB1(R)C14 (6.3%); and BSSS(R)C14 (7.0%)] also had the lowest percent stalk lodging population means when these populations were averaged across possible Design II and Reciprocal Design II crosses. The significantly negative GCA estimate of the BS28(R)C3 (-2.8%) population suggests that it contains favorable alleles for reduced stalk lodging (*i.e.*, stronger stalks) which accent the additive nature of the population's performance in crosses. The significantly negative GCA estimates of the BS28(R)C3 (-2.8%), BSSS(R)C14 (-1.2%), and BSCB1(R)C14 (-1.9%) populations were in agreement with those of Echandi and Hallauer (1996) of -2.5, -4.0, and -1.7%. A highly significantly negative SCA estimate of -3.7% and a significantly negative SCA estimate of -2.3% were calculated for the crosses BSK(S)C11 x BS29(R)C3 and BS28(R)C3 x BS16(S)C2 (Table C3). The highly significantly negative SCA estimate for BSK(S)C11 x BS29(R)C3 (-2.3%) contradicts the highly significantly positive GCA estimate calculated for BSK(S)C11 (5.0%). This implies that the non-additive nature, or dominance effects and differences in allele frequencies, in the intervarietal cross were supported more for reduced stalk lodging compared with the additive nature of the populations themselves. The heterotic combination BS28(R)C3 x BS29(R)C3, or Tuxpeño x Suwan-1, had a highly significantly positive SCA estimate of 3.1% indicating that stalk lodging increased by 3.1% when the cross was established. The significantly negative SCA estimate of the cross BS28(R)C3 x BS16(S)C2 (-2.3%) correlates with it having the lowest percent stalk lodging average of 3.6% calculated among both the Design II and Reciprocal Design II crosses.

In the combined analysis of variance, contrast statements used to evaluate sums of squares for the Stiff-Stalk maternal GCA effects, Non-Stiff-Stalk maternal GCA effects, and the Reciprocal SCA effect all showed non-significance ( $Pr > 0.05$ ) when analyzed for root lodging and stalk lodging (Table 3). However, significant differences were detected for the estimate statements used to calculate the corresponding maternal GCA and reciprocal SCA estimates for each effect between both traits (Table D2 and Table D3). Root lodging maternal GCA and reciprocal SCA estimate statements showed a significant reciprocal SCA estimate of -9.2% for the cross BSK(S)C11 x BS29(R)C3. This result indicates that the Design II cross, BSK(S)C11 x BS29(R)C3, results in 9.2% less root lodging compared with

the Reciprocal Design II cross BS29(R)C3 x BSK(S)C11. Stalk lodging estimate statements showed a Stiff-Stalk maternal GCA effect being significantly different from zero for the BSK(HI)C11 (1.9%) population. The significantly different GCA value of 1.9% suggests that when BSK(HI)C11 is used as the female parent in crosses, on average the crosses in the study containing the population will have 1.9% more stalk lodging compared with when the BSK(HI)C11 population is used as a male parent in crosses. Three significantly negative SCA estimates occurred for the cross combinations BSK(HI)C11 x BS26(S)C4 (-5.6%), BSK(S)C11 x BSCB1(R)C14 (-4.9%), and BSSS(R)C14 x BS29(R)C3 (-3.7%). These negative estimates suggest that the Design II crosses have a lower level of stalk lodging compared with the Reciprocal Design II cross.

Root lodging and Stalk lodging mid-parent heterosis and percent mid-parent heterosis values were calculated for a measure of heterosis separately for the 35 Design II crosses and 35 Reciprocal Design II crosses in the study (Table E3, Table E4, Table E5, and Table E6). Similar to GCA and SCA estimates, negative mid-parent heterosis and percent mid-parent heterosis estimates are desired for each population cross. Averaged over all Design II population crosses, the crosses had an average mid-parent heterosis estimate of 12.6% for root lodging and -8.7% for stalk lodging (Table 6). Root lodging mid-parent heterosis and percent mid-parent heterosis estimates ranged from a low of -6.0% and -18% for the cross BS34(S)C4 x BS26(S)C4 to a high of 8.6% and 56% for BS13(S)C9 x BSCB1(R)C14 (Table E3). Significant differences for root-lodging mid-parent heterosis estimates were not detected for the Design II population crosses in this study. The populations BS34(S)C4 and BSSS(R)C14 were the only two populations that had negative average percent mid-parent heterosis values of -11% and -1%, respectfully, across their respective crosses. These estimates suggest reduced root lodging means based on the percent mid-parent values and for the BSSS(R)C14 population average shows correlation with the BSSS(R)C14 population's low root lodging Design II mean (20.3%) averaged over crosses containing the population (Table A3). The cross BSSS(R)C14 x BSCB1(R)C14 had a negative estimate of percent mid-parent heterosis of -13% suggesting that 14 cycles of reciprocal recurrent selection had led to genetic divergence in both populations favoring selection for alleles contributing to reduced root lodging. On average, population crosses between two U.S. Corn Belt

populations had positive estimates of percent mid-parent heterosis (*i.e.*, BS10(FR)C14 x BS11(FR)C14), suggesting that the non-additive nature of the crosses allowed the expression of greater root lodging percentages.

Design II stalk lodging mid-parent heterosis and percent mid-parent heterosis estimates ranged from a low of -6.1% and -63% for BS28(R)C3 x BS16(S)C2 to a high of 2.7% and 45% for the cross BS34(S)C4 x BS29(R)C3 (Table E4). The negative mid-parent heterosis value of BS28(R)C3 x BS16(S)C2 (-6.1%) was the only value that was highly significantly different from zero and correlated with having the lowest mean stalk lodging value of 3.5% (Table A5). The two populations in the cross, BS28(R)C3 (-3.1% and -34%) and BS16(S)C2 (-2.3% and -23%), also had the two highest negative percent mid-parent heterosis cross combination averages among Design II crosses. Low mid-parent heterosis and percent mid-heterosis estimates for crosses containing BS28(R)C3 suggests that the population contains favorable alleles accenting potential for reduced stalk lodging. The cross BSK(HI)C11 x BS26(S)C4 (-32%) had the highest negative percent mid-parent heterosis estimate among U.S. Corn Belt populations, while the cross BSSS(R)C14 x BSCB1(R)C14 had a percent mid-parent heterosis estimate of 25%, which does not agree with the -33.3% mid-parent heterosis estimate of Echandi and Hallauer (1996).

Reciprocal Design II population crosses had average percent mid-parent heterosis estimates of 6.5% for root lodging and -8.1% for stalk lodging (Table 6). Root lodging mid-parent heterosis and percent mid-parent heterosis estimates ranged from a low of -8.0% and -23% for BS16(S)C2 to a high of 7.8% and 51% for the cross BSCB1(R)C14 x BS13(S)C9 (Table E4). Similar to Design II population crosses, no significant differences among root lodging mid-parent heterosis estimates were detected for the Reciprocal Design II population crosses. On average, root lodging mid-parent heterosis estimates and percent mid-parent heterosis root lodging population averages were lower across Reciprocal Design II crosses (1.2% and 7%) compared with Design II population crosses (2.1% and 13%) averages (Tables E3 and Table E4). However, the differences between Reciprocal Design II mid-parent heterosis estimates and Design II mid-parent heterosis estimates were not significant at the five percent level of significance. The populations BSSS(R)C14 (-1%) and BS34(S)C4 (-11%) remained as the only two populations having negative percent mid-parent heterosis

population averages. Based on Reciprocal cross percent mid-parent heterosis estimates, plant breeders may deviate away from normal crossing strategies and use Stiff-Stalk populations as male parents in crosses to get reduced amounts of root lodging in crosses.

Reciprocal Design II stalk lodging mid-parent heterosis and percent mid-parent heterosis values ranged from a low of -6.0% and -62% for the cross BS16(S)C2 x BS28(R)C3 to a high of 3.1% and 49% for BS29(R)C3 x BSSS(R)C14 (Table E6). Similar to the Design II cross BS28(R)C3 x BS16(S)C2 (-6.1%), the reciprocal cross BS16(S)C2 x BS28(R)C3 (-6.0%) showed a highly significant mid-parent heterosis estimate and also had the second lowest stalk lodging mean among Reciprocal Design II crosses. Another significant percent mid-parent heterosis estimate existed for the cross BS29(R)C3 x BSK(S)C11 (-43%) which had a stalk lodging mean (7.5%) lower than the overall stalk lodging cross mean of 8.2% (Table E6 and Table A6). Reciprocal Design II crosses containing 50% exotic germplasm on average had negative percent mid-parent heterosis estimates and in some combinations such as BS29(R)C3 x BSK(HI)C11 (-42%) had low stalk lodging means (5.0%) indicating the potential of exotic germplasm to contribute good agronomic stalk characteristics in crosses (Table E6 and Table A6). Some Reciprocal Design II crosses showed dramatic reductions or increases in stalk lodging percent mid-parent heterosis estimates when compared with the Design II crosses. The Reciprocal Design II cross BSCB1(R)C14 x BSSS(R)C14 (-1.5% and -27%) showed a significant reduction in mid-parent heterosis and percent mid-parent heterosis compared with the Design II cross BSSS(R)C14 x BSCB1(R)C14 heterosis estimates of 1.3% and 25%. The former estimate agrees closely with the -33.3% percent mid-parent heterosis estimate calculated by Echandi and Hallauer (1996).

These data suggest that recurrent selection programs have changed the way in which a population can be used in crosses, whereby some Stiff-Stalk populations normally used as females may give lower stalk lodging means when the population is used as a male parent in the crosses. A similar trend was identified earlier among the Stiff-Stalk and Non-Stiff-Stalk populations for the agronomic trait root lodging based on cross performance and population averages. In some respects, these trends of how the population is being used in crosses are the opposite of how industry is using the population in crosses.

### Plant Height and Plant Ear Height

Plant height and plant ear height means for the 35 Design II population crosses between Stiff-Stalk and Non-Stiff-Stalk populations and the 12 parent populations *per se* are presented in Table A7 and Table A9. Reciprocal Design II population crosses along with the 12 populations *per se* plant height and plant ear height means are presented in Table A8 and Table A9. Lower plant height and plant ear height means are usually desired by plant breeders when evaluating the agronomic performance of a hybrid maize plant or population. Plants with lower plant ear heights have the ear placed in the lower part of the stalk, which decreases potential stalk breakage and increases harvesting potential. Plants with lower plant heights spend less time developing vegetative growth and are able to expend more energy in ear development. Population *per se* and population cross agronomic performance indicators such as overall and reciprocal GCA and SCA estimates are usually desired to be negative indicating the potential of the population or the cross to transmit favorable alleles for reduced plant and plant ear heights (Table C4, Table C5, Table D4, and Table D5). Negative plant and plant ear height mid-parent heterosis and percent mid-parent heterosis estimates are also desired indicating reduced plant and plant ear height means compared with the mid-parent value (Table E7, Table E9, Table E8, and Table E10). Plant height and plant ear height means of the 12 populations *per se* will be discussed in detail.

Plant height means for the seven Stiff-Stalk populations ranged from a low of 191.3 cm for BS13(S)C9 to a high of 232.6 cm for BSSS(R)C14, while the Non-Stiff-Stalk populations ranged from a low of 204.6 cm for BSCB1(R)C14 to a high of 238.4 cm for BS26(S)C4 (Table A7). Plant ear height means for the Stiff-Stalk populations ranged from a low of 83.7 cm for BS13(S)C9 to a high of 116.8 cm for BS10(FR)C14, while Non-Stiff-Stalk populations ranged from a low of 87.5 cm for BSCB1(R)C14 to a high of 116.6 cm for BS26(S)C4 (Table A8). Average plant height and plant ear height means among all 12 parent populations were 218.4 cm and 103.2 cm, respectively (Table 6). The Stiff-Stalk population BS13(S)C9 (191.3 cm and 83.7 cm) and the Non-Stiff-Stalk population BSCB1(R)C14 (204.6 cm and 87.5 cm) both exhibited the two lowest plant height and plant ear height means suggesting that their respective recurrent selection programs have been successful in selecting plants exhibiting lower plant and plant ear heights. Interestingly, the

populations, BS10(FR)C14 (230.8 cm), BS11(FR)C14 (234.3 cm), and BSSS(R)C14 (232.6 cm), all advanced by 14 cycles of reciprocal recurrent selection, have plant heights greater than, and in some cases significantly different, from the adapted tropical populations which have undergone fewer cycles of recurrent selection (i.e., BS28(R)C3 (204.9 cm)). These results suggest that recurrent selection programs have also been beneficial in favoring alleles that transmit reduced plant and plant ear heights in those adapted tropical populations, but reciprocal recurrent selection has indirectly selected for increased plant and plant ear heights in some of the U.S. Corn Belt populations included in this study. Population plant and plant ear height means, despite being advanced by one or more cycles of recurrent selection, are slightly higher or lower, but similar to those plant and ear height estimates presented by Iglesias and Hallauer (1991), Echandi and Hallauer (1996), and Carena (1994).

Plant height means for the U.S. Corn Belt Cycle 0 populations ranged from a low of 222.0 cm for BSCB1C0 to a high of 241.7 cm for BS11C0 (Table 7). Both populations are listed within the Non-Stiff-Stalk group. Cycle 0 population plant ear height means ranged from 106.4 cm for BSCB1C0 to 134.2 cm for BS11C0. Highly significant differences among Cycle 0 populations were only detected for both traits in the Non-Stiff-Stalk populations. Plant height and plant ear height Cycle 0 population averages are 230.0 cm and 115.7 cm, respectively (Table 6).

Population improvement after ' $T$ ' cycles of recurrent selection was estimated by comparing plant height and plant ear height means of U.S. Corn Belt Cycle  $I$  and Cycle 0 populations (Table 8). The BS13(S)C9 population after seven cycles of half-sib and nine cycles of  $S_1$  recurrent selection showed the greatest significant reductions in plant height (-41.1 cm) and plant ear height (-31.9 cm) when compared to their Cycle 0 progenitor population BSSSC0. Significant reductions were detected for both agronomic traits across the remaining populations compared in the analysis; except for plant height in the BSSS(R)C14 population which showed a non-significant 0.3 cm increase in plant height. An interesting result occurred for the BS26(S)C4 population, which after four cycles of  $S_1$  selection, had a nonsignificant 4.8 cm increase in plant height and significant 7.9 cm increase in plant ear height. This can be explained by  $S_1$  selection having directly selected for increased plant and plant ear height within the BS26(S)C4 population. Mulamba *et al.*

(1983) reported a 16.6 cm for BSK(S)C8 and a 17.4 cm for BSK(HI)C8 reduction in ear height after eight cycles of selection from the BSKC0 population. The decreasing plant height and plant ear height trend of BSK(S)C11 and BSK(HI)C11 continues after 11 cycles of recurrent selection.

The 70 population crosses with a plant height mean of 232.9 cm showed a significant 14.5 cm increase, or 6.6% increase, in plant height over the population mean of 218.4 cm (Table 6). The average plant ear height of the 70 population crosses was 111.1 cm which showed a 8.0 cm or 7.7% increase in plant ear height over the population mean of 103.2 cm. The positive increases in plant height (6.6%) and plant ear height (7.7%) served as measures of average percent mid-parent heterosis between the population crosses and the parents *per se*. The positive increases in plant height and plant ear height also suggest that dominance effects and possibly epistatic effects resulted in greater plant height and plant ear height measures when the crosses were compared with the parents *per se*.

Design II population cross plant height means ranged from a low of 216.2 cm for BS28(R)C3 x BS16(S)C2 to a high of 246.3 cm for BSSS(R)C14 x BS26(S)C4 (Table A7). Plant ear height means for the 35 crosses varied from a low of 100.2 cm for BS28(R)C3 x BSCB1(R)C14 to a high of 120.8 cm for the cross BS10(FR)C14 x BS26(S)C4 (Table A9). Design II population cross averages calculated for the two traits were 232.5 cm for plant height and 111.1 cm for plant ear height (Table 6). Significant differences were detected among crosses for both plant height and plant ear height based on the  $LSD_{0.05}$  of 8.1 cm and 6.7 cm., respectfully. The lower plant height expressed by the cross BS28(R)C3 x BS16(S)C2 (246.3 cm) was also the only cross with a plant height lower than, but not significantly different from, the hybrid check plant height mean of 218.8 cm. The BS28(R)C3 (227.5 cm) and BS16(S)C2 (209.7 cm) populations used to make the cross also had two of the lower plant height population averages when in hybrid combination; whereas the cross with the highest plant height, BSSS(R)C14 x BS26(S)C4 (246.3 cm), had the two highest plant height population averages [BSSS(R)C14 (240.5 cm); BS26(S)C4 (237.8 cm)] derived from hybrid combination performance. On average, the BSCB1(R)C14 population had the lowest plant ear height average when in hybrid combination of 107.0 cm. Similarly, the inclusion of the BSCB1(R)C14 into the cross BS28(R)C3 x BSCB1(R)C14 also led to the

population cross having the lowest plant ear height among the other population crosses. The adapted exotic population BS28(R)C3 also had the third lowest plant ear height population average (107.8 cm) when in hybrid combination and the second lowest parent mean of 93.9 cm (Table A9); providing agreement with Hallauer (1994) stating that mass selection was successful for lower plant height and plant ear height in the populations.

Reciprocal Design II population crosses averages calculated over the 35 Reciprocal crosses was 232.6 cm for plant height and 110.9 cm for plant ear height (Table 6). As seen in the Design II crosses, the BS16(S)C2 population still had the lowest plant height population average when in hybrid combination of 220.2 cm (Table A8). The BS16(S)C2 population was also included in the cross BS16(S)C2 x BS13(S)C9 which had the lowest plant height among crosses of 209.7 cm. The cross BS16(S)C2 x BS13(S)C9 also had the lowest plant ear height among the crosses of 98.0 cm (Table A10). This is in partial agreement with Echandi and Hallauer's (1996) results indicating that BS16(S) population had lower plant and plant ear heights when crossed with U.S. Corn Belt cultivars rather than adapted tropical cultivars. The cross BSCB1(R)C14 x BS28(R)C3 had the second lowest plant height among the 35 crosses of 222.8 cm. While BS26(S)C4 x BS10(FR)C14 had the highest plant ear height of 120.5 cm, this correlates well with the results indicating that both populations involved (BS26(S)C4 and BS10(FR)C14) had above average plant ear height population averages when placed in hybrid combination (116.1 cm and 115.5 cm).

Significant differences were not detected among the Design II and the Reciprocal Design II population crosses averages for plant height and plant ear height based on the  $LSD_{0.05}$  values of 8.1 cm and 6.7 cm. Evaluation of population crosses through a separate analysis considering mean differences between Design II and Reciprocal Design II crosses, however, showed significant differences existing for both plant height and plant ear height (Table B4 and Table B5). The cross BSSS(R)C14 x BS29(R)C3 showed a highly significantly negative difference in plant height and plant ear height of -10.9 cm and -9.6 cm between the Reciprocal Design II cross and the Design II cross. Large, significantly, positive differences were observed for the cross BS13(S)C9 x BS16(S)C2 which showed plant height and plant ear height differences of 16.5 cm and 11.8 cm when comparing the Design II cross with the Reciprocal Design II cross.



Overall GCA and SCA estimates were calculated for plant height and the plant ear height across all 70 population crosses in the study (Table C4 and Table C5). The BS16(S)C2 population reported the largest significant negative GCA estimates for both plant height (-10.0 cm) and plant ear height (-4.8 cm). These results were confirmed by Iglesias and Hallauer (1991) which calculated a negative plant ear height GCA estimate of -5.2 cm for BS16(S)C2 suggesting that the population contains favorable alleles for shorter hybrid progenies when used in crosses. Significantly positive GCA estimates were observed in both plant height and plant ear height for the populations BS10(FR)C14 (3.1 cm and 4.8 cm), BSSS(R)C14 (8.8 cm and 2.7 cm), BS11(FR)C14 (2.9 cm and 1.6 cm), and BS26(S)C4 (6.5 cm and 4.8 cm). These populations correspondingly had greater plant height and plant ear height population averages when placed in hybrid combinations. The cross BS28(R)C3 x BSCB1(R)C14 had the largest negative SCA values for plant height (-5.5 cm) and plant ear height (-4.0 cm). The BS28(R)C3 x BSCB1(R)C14 cross SCA values for plant height is contradictory to the BSCB1(R)C14 (0.1 cm) population having a nonsignificant positive GCA value suggesting nonadditive effects in the population cross being more important than additive effects. However, a negative plant ear height SCA value for the cross BS28(R)C13 x BSCB1(R)C14 coincided with the lowest average plant ear height mean (99.9 cm) among all 70 crosses (Table A9 and Table A10). BS28(R)C3 x BS26(S)C4 was the only cross that reported positive significant SCA values for both plant height (7.4 cm) and plant ear height (3.1 cm), indicating that alleles in the intervarietal cross led to increased plant and ear heights in progenies.

Plant height and plant ear height Stiff-Stalk maternal, Non-Stiff-Stalk maternal, and Reciprocal SCA effects were calculated by examining the difference among Design II and Reciprocal Design II population cross averages and population crosses *per se*. Contrast statements used to calculate sums of squares for the combined analysis of variance indicated a significant Stiff-Stalk maternal GCA effect for plant height only; significant Non-Stiff-Stalk maternal GCA effects for plant height and plant ear height; and no significant Reciprocal SCA differences for either trait (Table 3). However, reciprocal differences were detected for some crosses based on the estimate statements used to calculate the actual SCA estimates among crosses for the two traits (Table D4 and Table D5). The Stiff-Stalk

population BS28(R)C3 showed a negative significant GCA estimate of -3.4 cm indicating that crosses including BS28(R)C3 were 3.4 cm shorter when the population was used as a female parent in the cross compared with its use as a male parent. The Non-Stiff-Stalk BS29(R)C3 population also showed a significantly negative GCA estimate of -3.6 cm for plant height. The Non-Stiff-Stalk population BS16(S)C2 showed positive maternal GCA estimates for both plant height (4.9 cm) and plant ear height (3.7 cm). Significantly positive reciprocal SCA estimates were detected for both plant height and plant ear height in the cross BS13(S)C9 x BS16(S)C2 (7.9 cm and 5.6 cm) suggesting that the Design II cross resulted in taller progenies compared with the Reciprocal Design II cross. Negative significant reciprocal SCA estimates were found for the crosses BS13(S)C9 x BS11(FR)C14 (-6.7 cm) and BS28(R)C3 x BS16(S)C2 (-6.8 cm) when examining the agronomic trait plant height.

Plant height and plant ear height average percent mid-parent heterosis values among Design II crosses were 6.6% and 8.0%, respectfully, while average percent mid-parent heterosis values among Reciprocal Design II crosses were 6.6% (plant height) and 7.8% (plant ear height) (Table 6). The populations BS13(S)C9 (23.8 cm and 12%; 15.4 cm and 16%) and BSCB1(R)C14 (23.6 cm and 11%; 12.9 cm and 14%) exhibited on average the greatest positive amount of mid-parent heterosis and percent mid-parent heterosis for both plant height and plant ear height when averaged over the Design II crosses that included the respective populations (Table E7 and Table E9). Coincidentally, the cross BS13(S)C9 x BSCB1(R)C14, which includes the two populations exhibiting the largest heterotic responses, had the highest mid-parent heterosis and percent mid-parent heterosis values of 34.9 cm and 18% for plant height and 21.6 cm and 25% for plant ear height. The lowest amount of mid-parent heterosis and percent mid-parent heterosis for plant height was expressed by the cross BS10(FR)C14 x BS26(S)C4 with only 2.7% and 1% percent mid-parent heterosis being observed. Similarly, the cross BSK(HI)C11 x BS29(R)C3 had the lowest level of mid-parent heterosis and percent mid-parent heterosis for plant ear height of -2.1 cm and -2 %. Although these values are nonsignificant, the small positive and negative heterosis estimates are valued by plant breeders since these estimates suggest that dominance effects within the crosses resulted in reduced plant height and plant ear height.

Among the Reciprocal Design II crosses, the populations BSCB1(R)C14 (23.3 cm and 11%; 12.6 cm and 14%) and BS13(S)C9 (20.1 cm and 10%; 12.8 cm and 14%) maintained the greatest positive mid-parent heterosis and percent mid-parent heterosis estimates when averaged over the crosses that included the two populations for both plant and plant ear height (Table E8 and Table E10). Within the Reciprocal Design II crosses, the cross BSCB1(R)C14 x BS13(S)C9 still showed the greatest positive change in plant height and plant ear height mid-parent heterosis and percent mid-parent heterosis estimates with values of 30.7 cm and 15% and 18.8 cm and 22% respectfully. The Stiff-Stalk and Non-Stiff-Stalk populations BS10(FR)C14 (4.3 cm and 4%; 8.8 cm and 4%) and BS16(S)C2 (4.2 cm and 4%; 8.4 cm and 4%) populations both showed on average the lowest amount of mid-parent heterosis and percent mid-parent heterosis for plant height and plant ear height when averaged over all crosses including the two populations. The low heterosis estimates obtained for plant height for both populations were nonsignificant, but the low heterosis estimates for plant height were significant.

#### **Pollen Date and Silk Date**

Pollen date and silk date means of the 35 Design II population crosses between Stiff-Stalk and Non-Stiff-Stalk populations and for the 12 parent populations *per se* are presented in Table A11 and Table A13. Reciprocal Design II population cross pollen date and silk date means are presented in Table A12 and Table A14. Pollen date and silk date means are expressed as the number of days after planting to which 50% of plants in the plot are shedding pollen or silks. The pollen date and silk date of a population *per se* or population cross provides an indication of agronomic performance regarding the relative maturity of that particular population or population cross. A lower mean number of days to pollen shed and silk shedding along with negative GCA, SCA, and mid-parent and percent mid-parent heterosis estimates are desirable since these indicators lead to earlier maturity populations and population crosses. Pollen dates and silk dates of the 12 parent populations *per se* will be discussed next.

Pollen date means for the seven Stiff-Stalk populations ranged from a low of 70.0 days for BS28(R)C3 to a high of 74.0 days after planting for BS13(S)C9, while for Non-Stiff-Stalk populations pollen dates ranged from a low of 68.5 days for BS16(S)C2 to a high

of 74.9 days for BS29(R)C3 (Table A11). Silk date means for the Stiff-Stalk populations ranged from a low of 72.0 days for BS28(R)C3 to a high of 76.1 days for BSSS(R)C14, while silk dates for Non-Stiff-Stalk populations ranged from a low of 72.0 days for BS16(S)C2 to a high of 76.4 days for BS29(R)C3 (Table A13). An overall average pollen date and silk date among the 12 populations *per se* was 72.4 days and 74.6 days, respectively (Table 6). Significant differences were detected among the populations *per se* for both pollen date and silk date based on the  $LSD_{0.05}$  of 1.1 days and 1.2 days after planting. The population BS28(R)C3 had a mean pollen date (70.0 days) and silk date (72.0 days) significantly earlier in days to pollen shed compared with the check hybrid based on the  $LSD_{0.05}$ . The U.S. Corn Belt populations BS10(FR)C14, BS13(S)C9, BS11(FR)C14, and BSSS(R)C14 had pollen dates and silk dates on average 1 to 2 days later than the parental averages (Table A11 and Table A13). Similar trends in silk dates for these U.S. Corn Belt populations, despite these populations having undergone one or more cycles of recurrent selection since the time of previous studies were observed by Michelini and Hallauer (1993) and Echandi and Hallauer (1996).

Pollen date means for the U.S. Corn Belt Cycle 0 populations ranged from a low of 70.1 days for BSCB1C0 to a high of 74.0 days for BSKC0 (Table 7). Silk date means among the Cycle 0 populations ranged from a low of 73.5 days for BSCB1C0 to a high of 80.2 days for BS11C0. Highly significant differences were detected for both traits among the Stiff-Stalk and Non-Stiff-Stalk Cycle 0 populations based on the  $LSD_{0.05}$  (1.1 days and 1.2 days). The average pollen date and silk date of Cycle 0 populations was 72.3 days and 76.1 days, respectively (Table 6).

Improvement in population performance after '*I*' cycles of recurrent selection was estimated by comparing pollen date and silk date means of U.S. Corn Belt Cycle *I* and Cycle 0 populations (Table 8). The BSK(S)C11 population showed the largest significant decrease in pollen date of -2.4 days when the BSK(S)C11 population was compared with the BSKC0 population. A highly significant reduction in silk date of 5.5 days was observed in the BS11(FR)C14 population after 14 cycles of full-sib reciprocal recurrent selection, suggesting that deleterious alleles causing delayed silking were reduced through the use of the recurrent selection program. However, the BS10(FR)C14 (2.0 days) population and the BS13(S)C9

(2.1 days) population both showed significant increases in pollen date compared with their respective progenitor populations following 'I' cycles of recurrent selection.

A measure of average heterosis was estimated by evaluating the mean performance of the population crosses compared with the parents. The Design II and Reciprocal Design II population crosses with a mean pollen date of 71.9 days showed a 0.5 day reduction or 0.6% improvement over the parental pollen date mean of 72.3 days (Table 6). The population crosses with a silk date mean of 74.0 days also showed a 0.6 day reduction or 0.8% improvement compared with the parental silk date mean of 74.6 days. The 0.6% and 0.8% improvements in pollen date or silk date, which served as estimates of average heterosis, were nonsignificant at the five percent level of significance in the combined analysis of variance (Table 3).

Pollen date of the 35 Design II population crosses ranged from a low of 69.3 days for the cross BS28(R)C3 x BS16(S)C9 to a high of 73.9 days for the cross BS13(S)C9 x BS26(S)C4 (Table A11). Silk dates among the Design II crosses ranged from a low of 71.5 days for BSK(HI)C11 x BSCB1(R)C14 to a high of 76.2 days for the cross BS34(S)C4 x BS26(S)C4 (Table A13). Significant differences in pollen date and silk date existed among the Design II crosses based upon the  $LSD_{0.05}$  of 1.1 days and 1.2 days. Average days to 50 percent pollen shed and 50 percent silk shed among the 35 crosses were 72.0 days and 73.8 days, respectfully (Table 6). The fewer number of days to 50% pollen shed for the cross BS28(R)C3 x BS16(S)C2 (69.3 days) was also significantly lower than the hybrid check pollen date of 71.7 days. The two adapted tropical populations deriving the cross, BS28(R)C3 (71.1 days) and BS16(S)C2 (70.4 days), also had the two lowest pollen date population averages when in hybrid combination. These estimates imply that both cultivars showed favorable alleles for earlier maturity in terms of pollen shed and may provide potential germplasm sources for bringing earliness into U.S. Corn Belt population crosses. The two U.S. Corn Belt populations BS13(S)C9 and BS26(S)C4, which had the longest days to pollen shed among crosses, also maintained two of the longer average population silk dates (74.1 days and 74.4 days) suggesting that the populations provide alleles for delayed maturity (Table A11 and A13). Nonadditive effects derived from cross performance caused the BSK(HI)C11 x BSCB1(R)C14 cross to have the earliest silk date (71.5 days) along with

two of the earliest average population silk dates (73.0 days and 73.3 days) compared with the other populations. The BSK(HI)C11 x BSCB1(R)C14 cross also exhibited a silk date significantly lower than the hybrid check silk mean of 72.9 days. U.S. Corn Belt populations BS10(FR)C14, BSSS(R)C14, and BS11(FR)C14 all had population silk date averages similar to the Design II population average of 73.8 days (Table A13). Crosses derived among these aforementioned populations, such as BSSS(R)C14 x BSCB1(R)C14 and BS10(FR)C14 x BSK(HI)C11, had silk dates (73.2 days and 74.7 days) that corresponded with silk dates posted by Michelini and Hallauer (1993) and Echandi and Hallauer (1996).

The Reciprocal Design II cross BS16(S)C2 x BSK(HI)C11 had the earliest pollen date taking 73.9 days to achieve 50% of the plants shedding pollen from tassels (Table A12). The BS16(S)C2 x BSK(HI)C11 cross's pollen date was also significantly earlier than the hybrid check's pollen date of 71.7 days. Similar to Design II crosses, crosses containing the BS16(S)C2 population on average had the earliest pollen date with a population average of 70.4 days. The reciprocal cross BS26(S)C4 x BS13(S)C9 took the longest number of days to achieve 50 percent pollen shed among plants due to dominance effects within the population cross resulting in delayed maturity. Crosses containing the U.S. Corn Belt populations BS10(FR)C14 (72.0 days), BS13(S)C9 (71.7 days), BS11(FR)C14 (71.4 days), and BSCB1(R)C14 (71.1 days) on average had pollen dates similar to the Reciprocal Design II cross mean of 71.8 days. Silk dates among Reciprocal Design II crosses ranged from a low of 71.8 days for the cross BS16(S)C2 x BSK(S)C11 to a high of 77.8 days for the cross BS26(S)C4 x BS34(S)C4 (Table A14). Crosses containing the population BS16(S)C2, an adapted tropical population, had the earliest population silk date average taking 72.1 days to get 50% of the plants having emerged silks. This result suggests that the BS16(S)C2 population can be used to bring earlier silking capabilities into population crosses. The cross with the latest silk date BS26(S)C4 x BS34(S)C4 (77.8 days) contained the only two populations that when averaged over crosses had significantly later silk dates [BS26(S)C4 (75.5 days); BS34(S)C4 (75.2 days)] compared with the Reciprocal Design II cross average of 74.1 days. Significant differences in silk dates were observed among Reciprocal Design II crosses based on the  $LSD_{0.05}$  of 1.2 days.

Mean differences between Design II and Reciprocal Design II population cross averages were not detected for the traits pollen date and silk date based on their respective LSD's. A separate analysis using contrasts to determine significant mean differences among Design II and Reciprocal Design II population crosses *per se* also showed nonsignificance for both pollen date and silk date. However, estimate statements used to determine the difference for each specific cross did show a significant difference in pollen date for the cross BSSS(R)C14 x BS16(S)C2 of -2.4 days (Table B6). This estimate implies that the Design II cross, BSSS(R)C14 x BS16(S)C2, was 2.4 days earlier than the Reciprocal Design II cross BS16(S)C2 x BSSS(R)C14. Significant mean differences in silk date estimates were also reported for the crosses BS10(FR)C14 x BS16(S)C2 (-2.3 days), BSSS(R)C14 x BS11(FR)C14 (-2.1 days), and BS28(R)C2 x BS26(S)C4 (-4.0 days) (Table B7).

Overall Stiff-Stalk and Non-Stiff-Stalk GCA and SCA estimates were calculated across all 70 population crosses for both the traits pollen date and silk date (Table C6 and Table C7). Significant differences were reported among the GCA and SCA estimates for both traits. The population BS16(S)C2 reported the largest significant negative GCA estimates for both pollen date (-1.4 days) and silk date (-1.0 days). These estimates imply that the additive nature of the populations when placed in cross combinations resulted in crosses that had a pollen date 1.4 days earlier and a silk date 1.0 days earlier in terms of relative maturity of the crosses. The populations, BS28(R)C3 and BSK(HI)C11, also showed significantly negative GCA estimates for both pollen date (-0.9 days and -0.7 days) and silk date (-0.8 days and -0.8 days). However, the populations BS26(S)C4 and BS29(R)C3 showed significant positive GCA estimates for both pollen date (1.1 days and 0.9 days) and silk date (1.0 days and 0.7 days). Prior to three cycles of recurrent selection, Echandi and Hallauer (1996) reported a positive silk date GCA estimate of 2.7 days in their study, which has since been reduced to a positive GCA estimate of 0.7 days (Table C7). A negative silk date GCA estimate of -1.0 days was reported by Echandi and Hallauer for the BSCB1(R)C12 population which is slightly larger than the negative GCA estimate of -0.6 days for BSCB1(R)C14 after two more cycles of recurrent selection in this study. Significantly negative SCA estimates for both pollen date and silk date were reported for the cross BS34(S)C4 x BS11(FR)C14 (-1.6 days and -1.6 days) suggesting that favorable alleles for

earlier maturity were present when these two populations existed in a cross combination. The cross BS10(FR)C14 x BS11(FR)C14, however, had significantly positive SCA estimates for both pollen date and silk date (0.9 days and 0.9 days) suggesting that full-sib reciprocal recurrent selection has resulted in increased maturity within this population cross.

Stiff-Stalk maternal GCA effects, Non-Stiff-Stalk maternal GCA effects, and Reciprocal SCA effects calculated by contrast statements were determined nonsignificant for both the pollen date and silk date agronomic traits (Table 3). However, estimate statements used to derive the GCA and SCA values detected a silk date Non-Stiff-Stalk maternal GCA effect and silk date reciprocal SCA effects being significant in the crosses (Table D7). A significantly negative maternal GCA effect was observed for the Non-Stiff-Stalk population BS26(S)C4 with an estimate of -0.7 days. This negative value predicts that cross performance using the population as a male parent (Design II crosses) is 0.7 days earlier in silk date cross performance verses when the population is used as a female parent (Reciprocal Design II crosses) in crosses. Significant negative reciprocal SCA estimates were observed for silk date among the crosses BS28(R)C3 x BS26(S)C4, BS34(S)C4 x BS29(R)C3, and BS10(FR)C14 x BS16(S)C2 (-2.9 days, -2.0 days, and -1.8 days, respectfully). For the crosses, the Design II crosses resulted in an earlier silk date compared with the Reciprocal Design II crosses. Information from the estimation of maternal GCA and Reciprocal SCA effects may provide information into how the populations based on cross performance may be used in crosses in the future.

Pollen date and silk date mid-parent heterosis and percent mid-parent heterosis values were calculated to provide a measure of the amount of heterosis obtained for the Design II and Reciprocal Design II cross compared with the mid-parent value (Table E11, Table E12, Table E13, Table E14). Design II population crosses had an average percent mid-parent heterosis of -0.6 days for pollen date and -1.1 days for silk date (Table 6). Design II pollen date mid-parent heterosis and percent mid-parent heterosis estimates ranged from a low of -2.0 days and -3% for the cross BS34(S)C4 x BS11(FR)C14 to a high of 2.0 days and 3% for the cross BS28(R)C3 x BS26(S)C4 (Table E11). All pollen date Design II mid-parent heterosis values were nonsignificant due to only a small decrease or increase in pollen date for the cross compared with the mid-parent value. This same premonition led to



nonsignificant estimate of average heterosis being calculated earlier for pollen date (Table 3). The U.S. Corn Belt populations BS10(FR)C14, BS13(S)C9, BSK(HI)C11, BSSS(R)C14, BS11(FR)C14, and BSCB1(R)C14 on average all expressed a percent mid-parent heterosis value of -1% based on the average of that population in cross combination (Table E11).

Design II silk date mid-parent heterosis values and percent mid-parent heterosis values ranged from a low of -3.2 days and -4% for BS28(R)C3 x BS26(S)C4 to a high of 1.6 days and 2% for the cross BS34(S)C4 x BSCB1(R)C14 (Table E13). The cross BS28(R)C3 x BS26(S)C4, exhibiting the lowest heterosis values, and the cross BSSS(R)C14 x BS11(FR)C14 (-2.6 days and -3%) both showed significant differences from zero when evaluated against the other Design II cross silk date heterosis values. Percent mid-parent heterosis estimated for pollen date and silk date fluctuated higher or lower compared with pollen date percent mid-parent heterosis estimates by Micheline and Hallauer (1993) and silk date percent mid-parent heterosis estimates by Echandi and Hallauer (1996) due to differences in growing season between the different studies. Fewer days to 50% pollen shed and 50% silk shed were observed in this study due to a possible later planting date which decreased the number of days necessary for plants to achieve anthesis and flowering capacities.

The Reciprocal Design II crosses had an average percent mid-parent heterosis estimate of -0.8 days for pollen date and a -0.7 day estimate for silk date (Table 6). On average, reciprocal crosses showed a greater average percent heterosis estimate for pollen date (-0.8 days verses -0.6 days) and a decreased average percent mid-parent heterosis estimate for silk date (-0.7 days verses -1.1 days) compared with the Design II crosses (Table E11, Table E13, Table E12, Table E14). Pollen date mid-parent heterosis and percent mid-parent heterosis values ranged from a low of -3.7 days and 5% for the cross BS11(FR)C14 x BS13(S)C9 to a high of 2.1 days and 3% for the cross BS16(S)C2 x BSSS(R)C14 (Table E13). The low and high mid-parent and percent mid-parent heterosis estimates for the crosses BS11(FR)C14 x BS13(S)C9 and BS16(S)C2 x BSSS(R)C14 both showed heterosis responses significantly different from zero for the trait pollen date (-3.7 days and -5%; 2.1 days and 3%). The cross BSCB1(R)C14 x BSK(HI)C11 showed a significantly negative mid-parent heterosis and percent mid-parent heterosis estimate of -2.2 days and -3% which

corresponded with the cross having the earliest Reciprocal Design II pollen date of 69.0 days in the study (Table A12).

Silk date mid-parent and percent mid-parent heterosis estimates for Reciprocal Design II crosses ranged from a low of -1.8 days and -2% for the cross BS29(R)C3 x BS10(FR)C14 to a high of 1.8 days and 2% for the cross BS26(S)C4 x BS34(S)C4 (Table E14). No significant differences were reported among the silk date mid-parent heterosis and percent mid-parent heterosis estimates due to small incremental differences existing between the cross and the corresponding mid-parent value. Based on the average of crosses that included BS13(S)C9, BS13(S)C9 was the only population that had mid-parent heterosis and percent mid-parent heterosis estimates increase from values of -0.9 days and -1% in Design II crosses to -1.2 days and -2% for Reciprocal Design II crosses (Table E12 and Table E14). These heterosis estimates may possibly suggest that the performance of BS13(S)C9 being used as a male for earlier maturity should place the population into the Non-Stiff-Stalk heterotic group.

## CONCLUSIONS

Seven Stiff-Stalk populations and five Non-Stiff-Stalk populations were placed into a Design II mating design to develop 35 Design II crosses and 35 Reciprocal Design II crosses to be evaluated for agronomic performance under U.S. Corn Belt environmental conditions. The 12 populations were categorized into the respective groups based on previously known maize heterotic group classifications and agronomic data collected from prior studies. Populations included within the two groups varied from U.S. Corn Belt populations to adapted tropical populations and all populations have been advanced by two or more cycles of recurrent selection.

The Design II analysis was successful to evaluate population performance *per se*, to determine possible new heterotic combinations between the 12 populations while maintaining existing heterotic patterns, and to allow for the expression of heterosis among the Design II and Reciprocal Design II crosses. The inclusion of reciprocal crosses into the study allowed for the identification of possible maternal and reciprocal effects that existed among the populations *per se* or the population crosses. The Design II analysis partitioned the crosses sums of squares into the following cross effects: Stiff-Stalk, Non-Stiff-Stalk, Stiff-Stalk x Non-Stiff-Stalk interaction, Stiff-Stalk maternal, Non-Stiff-Stalk maternal, and Reciprocal effects. Significant differences were observed for all agronomic traits evaluated for the Stiff-Stalk, Non-Stiff-Stalk, and Stiff-Stalk x Non-Stiff-Stalk interaction cross effects. Inferences taken from the significance of these cross effects allowed for the calculation of overall estimates of GCA for Stiff-Stalk and Non-Stiff-Stalk populations and an estimate of SCA for the Stiff-Stalk x Non-Stiff-Stalk interaction. The Design II analysis also showed significant differences existing in grain yield and plant height for the Stiff-Stalk maternal effect and plant and plant ear height for the Non-Stiff-Stalk maternal effect. Reciprocal cross effects for each trait were all nonsignificant. However, estimate statements used to estimate each individual maternal GCA and reciprocal SCA effect detected significant differences in grain yield, grain moisture, stalk lodging, and plant height for the Stiff-Stalk maternal effect, plant height, plant ear height and silk date for the Non-Stiff-Stalk maternal effect, and reciprocal effects for all traits except pollen date.

Estimates of average heterosis were expressed for grain yield, plant height and plant ear height in a non-orthogonal comparison between the 70 population crosses and the parents in the combined analysis. Average heterosis estimates are of importance to plant breeders due to suggesting that nonadditive genetic effects occurred within the crosses for these traits. Expression of heterosis for yield was evident as all mid-parent heterosis estimates among all 70 population crosses were significantly different from zero. Significant mid-parent heterosis estimates varied in number for the other agronomic traits evaluated in the study.

Evaluation of population *per se* performance indicated that Stiff-Stalk Cycle I populations and Non-Stiff-Stalk Cycle I populations *per se* achieved similar levels of grain yield and grain moisture along with having similar pollen dates and silk dates. However, the Stiff-Stalk populations on average showed slightly decreased levels of root lodging and stalk lodging and had a lower plant height and plant ear height. Overall U.S. Corn Belt population *per se* performance deviated for each trait being considered, but the BS10(FR)C14 population expressed the highest grain yield among the 12 populations evaluated. Adapted exotic populations in the study achieved average grain yield, root lodging, plant height, plant ear height, pollen date, and silk date means similar to U.S. Corn Belt populations that are more advanced by recurrent selection programs. Among the adapted exotic populations, BS29(R)C3 expressed a grain yield similar to the U.S. Corn Belt BS11(FR)C14 population which has undergone 14 cycles of reciprocal recurrent selection. These results suggest that recurrent selection programs have been successful in adapting tropical populations to the U.S. Corn Belt area and that these populations are potential sources of germplasm containing favorable alleles that may enhance agronomic performance of U.S. Corn Belt populations.

Further, Stiff-Stalk and Non-Stiff-Stalk population *per se* performance was illustrated through examination of overall GCA effects. Highly significant overall GCA effects for grain yield in the Stiff-Stalk BSSS(R)C14, BS10(FR)C14, and BS13(S)C9 populations, all composed of Reid Yellow Dent germplasm, and the Non-Stiff-Stalk BSCB1(R)C14 population, composed of Lancaster Sure Crop germplasm, suggest that these populations will result in increased population cross grain yields when each respective population is placed in cross combination. High and low overall GCA effects varied between the populations for each trait considered, but on average populations composed of Reid Yellow Dent or

Lancaster Sure Crop germplasm usually had the highest overall GCA estimates when averaged over all population crosses. Hallauer (1997a) stated the dramatic use of Reid Yellow Dent and Lancaster Sure Crop germplasm was due to their highly additive nature or their ability to combine well with other populations in cross formation. These conclusions offer confirmation to the above reasoning. These same populations also exhibited on average the highest population average mid-parent heterosis and percent mid-parent heterosis estimates when averaged over respective crosses.

Reciprocal Design II population crosses on average exhibited a slightly higher grain yield mean compared with the Design II population crosses average grain yield. Reciprocal Design II and Design II population crosses had very similar average means for all remaining agronomic traits evaluated in the study. Coincidentally, Reciprocal Design II population crosses exhibited slightly higher average percent mid-parent heterosis estimates for grain yield, grain moisture, plant height, and pollen date, while showing a slight mean decrease in root lodging, stalk lodging, plant ear height, and silk date. Population cross population averages were examined for significant mean differences between Design II and Reciprocal Design II crosses for each trait evaluated using the corresponding  $LSD_{0.05}$  for that trait. No significant differences between population cross averages were detected for all agronomic traits evaluated.

Significant mean differences between Design II and Reciprocal Design II population crosses *per se* were evaluated in a separate combined analysis in which significant differences between Design II and Reciprocal Design II means were reported for the traits grain moisture, plant height, and plant ear height. Estimate statements used to calculate each mean difference, however, detected significant differences for all traits evaluated. Considering grain yield, the crosses BS13(S)C9 x BS11(FR)C14 and BS13(S)C9 x BS16(S)C9 showed increased grain yields when BS13(S)C9 was used as a male parent in the cross verses being used as a female parent. Results from significant mean differences being observed among Design II and Reciprocal Design II crosses for grain yield and other agronomic traits evaluated provides evidence regarding how a population is used in population crosses. Recombination of alleles within the population with each successive

cycle of recurrent selection is selecting for both female and male plant characteristics enabling a population normally used as a female to be used as a male parent and vice versa.

The cross BS10(FR)C14 x BS29(R)C3 (Suwan-1 germplasm) had the highest average grain yield ( $7.96 \text{ t ha}^{-1}$  or  $127.4 \text{ bu acre}^{-1}$ ) when averaged over both the Design II population cross and the Reciprocal Design II cross. The BS10(FR)C14 x BS29(R)C3 cross also exhibited a highly significant grain yield SCA estimate. The large SCA value and corresponding high grain yield of the cross BS10(FR)C14 x BS29(R)C3, or Reid Yellow Dent x Suwan-1, is a result of non-additive effects occurring when the cross is developed. The cross combination should be considered as a new heterotic combination that could be placed into a long-term reciprocal recurrent selection program for the development and continued selection of advanced progenies for the development and selection of inbred lines. The Suwan-1 population, an adapted exotic population, could also provide genetic diversity through novel alleles that are not present currently within the U.S. Corn Belt population BS10(FR)C10.

Heterotic patterns among the population crosses were also maintained with the high average grain yield expressed by the cross BSSS(R)C14 x BSCB1(R)C14. The Stiff-Stalk population BSSS(R)C14 (Reid Yellow Dent germplasm) and BSCB1(R)C14 (Lancaster Sure Crop germplasm) together in a cross are part of the well-known and well-used heterotic pattern Reid Yellow Dent by Lancaster Sure Crop. Fourteen cycles of reciprocal recurrent selection have been performed between the populations implying that the frequency of favorable alleles for increased yield have been selected within both populations. The BSSS(R)C14 x BSCB1(R)C14 cross exhibited the highest mid-parent heterosis and percent mid-parent heterosis estimates among the crosses. The existence of other known heterotic patterns, such as the adapted exotic BS28(R)C3 x BS29(R)C3 (Tuxpeno x Suwan-1) heterotic pattern and the advanced U.S. Corn Belt BS10(FR)C14 x BS11(FR)C14 (Reid Yellow Dent x Lancaster Sure Crop) heterotic pattern was not as evident for grain yield and other agronomic traits.

A significant Stiff-Stalk maternal effect was observed for the trait grain yield. Stiff-Stalk maternal GCA estimates indicated that the Stiff-Stalk population BS13(S)C9 (Reid Yellow Dent germplasm) resulted in higher grain yields when the population was used as a

male parent in crosses versus being used as a female parent in crosses. The role of BS13(S)C9 being used as a male parent is the exact opposite of how industry uses lines developed from the population to produce single-cross hybrids. Based on the significance of Design II effects, another significant Stiff-Stalk maternal effect in plant height was detected for the BS28(R)C3 population in which shorter progenies resulted when the population was used as a female parent in crosses. Both populations in respective crosses also exhibited significant mean differences for grain yield between Design II and Reciprocal Design II crosses. Non-Stiff-Stalk maternal effects for plant height were reported for the populations BS16(S)C2 and BS29(R)C3, while a plant ear height Non-Stiff-Stalk maternal effect was detected for the BS16(S)C2 population.

The effect of recurrent selection on U.S. Corn Belt populations was evaluated by comparing Cycle *I* parent populations to Cycle 0 parent populations. Grain yield increased significantly for the Cycle *I* populations BS10(FR)C14 ( $2.18 \text{ t ha}^{-1}$ ), BS11(FR)C14 ( $1.51 \text{ t ha}^{-1}$ ), and BSSS(R)C14 ( $1.30 \text{ t ha}^{-1}$ ) from the Cycle 0 population after 14 cycles of reciprocal recurrent selection (Table 8). However, a nonsignificant decrease of  $0.23 \text{ t ha}^{-1}$  resulted after 14 cycles of reciprocal recurrent selection in the BSCB1(R)C14 population. These results imply that reciprocal recurrent selection was effective on favorable alleles for increased grain yield in the former three populations, but selection was not effective for favorable alleles for grain yield increases in the BSCB1(R)C14 population. Reciprocal recurrent selection, however, emphasizes selection on the population cross; hence, any changes in the populations themselves would be an indirect, or correlated, effect with selection on cross performance. Significant differences were also observed among each parent/cycle comparison for all remaining traits evaluated in the study.

Assumptions and findings collected from this Design II study were developed from agronomic data collected during only one year at six locations throughout central and southern Iowa. Extreme dry and hot environmental conditions, along with insect problems, during the 2002 growing season led to the Lewis location being discarded early in the summer. Conclusions from this experiment will be reinforced by conducting the experiment another year during normal U.S. Corn Belt Conditions, if attainable, to provide validity to the results achieved in predicting heterotic patterns and determining population performance in

crosses. Replication of the experiment may provide evidence for determining the BS10(FR)C14 x BS11(FR)C14 and BS28(R)C3 x BS29(R)C3 heterotic patterns that failed to be observed in this experiment. Failure to detect the aforementioned heterotic patterns was also observed by Echandi and Hallauer (1996).



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**APPENDIX A**

**DESIGN II AND RECIPROCAL DESIGN II POPULATION CROSS MEANS AND  
PARENTS *PER SE* AVERAGED OVER ENVIRONMENTS FOR DIFFERENT  
AGRONOMIC TRAITS**

Table A1. Grain moisture of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

and the 12 populations per se using combined SN and common means										
Populations	SS Females (A)‡									
	----- U.S. Corn Belt -- (1)§ -----					- Adapted Exotic -- (2) -				
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
----- % -----										
BS11(FR)C14	(1)	18.5	18.4	19.1	19.1	18.2	18.7	20.4	18.9	18.1
BS26(S)C4	(1)	19.8	19.8	20.0	19.7	20.1	20.0	21.9	20.2	20.4
BSCB1(R)C14	(1)	18.2	18.7	19.4	19.3	18.9	18.7	21.1	19.2	18.4
BS16(S)C2	(2)	19.5	19.6	20.7	19.7	19.4	19.7	21.1	19.9	20.1
BS29(R)C3	(2)	20.2	20.8	21.5	20.8	20.3	20.5	21.9	20.8	22.0
Average		19.2	19.4	20.1	19.7	19.4	19.5	21.3	19.8	19.8
Parent mean		18.9	18.8	20.0	19.6	18.9	18.9	23.4	19.8	19.8

† LSD<sub>(0.05)</sub> is 0.5 % for crosses and 0.6 % for parents *per se* within the crosses. Check grain moisture mean: LH198 x LH185 = 17.8 %.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A2. Grain moisture of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
NSS Females (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean	
	----- % -----									
BS11(FR)C14	(1)	18.6	18.0	19.6	18.4	18.5	18.7	20.3	18.9	18.1
BS26(S)C4	(1)	19.7	20.1	20.5	20.0	19.8	20.4	21.8	20.3	20.4
BSCB1(R)C14	(1)	18.5	18.6	19.1	18.8	18.8	18.6	20.6	19.0	18.4
BS16(S)C2	(2)	19.5	19.3	20.7	19.6	19.6	20.0	20.7	19.9	20.1
BS29(R)C3	(2)	19.9	20.8	21.6	20.7	20.8	20.9	22.4	21.0	22.0
Average		19.2	19.4	20.3	19.5	19.5	19.7	21.2	19.8	19.8
Parent mean		18.9	18.8	20.0	19.6	18.9	18.9	23.4	19.8	19.8

† LSD<sub>(0.05)</sub> is 0.5 % for crosses and 0.6 % for parents *per se* within the crosses. Check grain moisture mean: LH198 x LH185 = 17.8 %.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A3. Root lodging of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.<sup>†</sup>

Populations		SS Females (A)‡								
		----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -				
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
----- % -----										
BS11(FR)C14	(1)	26.7	22.0	33.7	25.6	20.1	24.4	37.1	27.1	27.3
BS26(S)C4	(1)	25.4	16.2	33.5	21.2	17.0	25.6	26.5	23.6	17.9
BSCB1(R)C14	(1)	28.1	23.8	30.5	30.5	17.8	26.7	31.0	26.9	24.7
BS16(S)C2	(2)	21.5	20.0	24.3	23.2	23.7	29.7	30.7	24.7	21.9
BS29(R)C3	(2)	25.4	25.3	30.1	22.9	22.8	28.3	35.5	27.2	32.8
Average		25.4	21.5	30.4	24.6	20.3	26.9	32.1	25.9	24.9
Parent mean		18.3	5.8	30.3	21.8	16.3	19.2	47.1	22.7	23.6

<sup>†</sup> LSD<sub>(0.05)</sub> is 10.1 % for crosses and 15.1 % for parents *per se* within the crosses. Check root lodging mean: LH198 x LH185 = 16.9 %.

<sup>‡</sup> The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

<sup>§</sup> U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A4. Root lodging of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
NSS Females (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
----- % -----										
BS11(FR)C14	(1)	25.0	18.1	34.7	25.8	23.7	29.3	37.5	27.7	27.3
BS26(S)C4	(1)	20.8	9.5	25.4	16.7	19.7	28.2	28.5	21.2	17.9
BSCB1(R)C14	(1)	21.6	23.0	35.2	23.5	16.5	25.5	34.3	25.7	24.7
BS16(S)C2	(2)	22.8	15.2	22.6	21.2	17.6	30.7	26.6	22.4	21.9
BS29(R)C3	(2)	25.1	21.5	34.6	33.2	18.8	30.0	32.3	27.9	32.8
Average		23.0	17.5	30.5	24.1	19.3	28.7	31.9	25.0	24.9
Parent mean		18.3	5.8	30.3	21.8	16.3	19.2	47.1	22.7	23.6

† LSD<sub>(0.05)</sub> is 10.1 % for crosses and 15.1 % for parents *per se* within the crosses. Check root lodging mean: LH198 x LH185 = 16.9 %.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A5. Stalk lodging of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

and the 12 populations per se using combined environmental means.											
Populations		SS Females (A)‡								Average	Parent mean
		----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4			
----- % -----											
BS11(FR)C14	(1)	8.1	8.6	12.2	16.5	7.4	4.8	7.4	9.3	11.8	
BS26(S)C4	(1)	11.1	10.2	8.2	16.5	6.5	6.9	8.3	9.7	14.0	
BSCB1(R)C14	(1)	5.2	6.0	7.6	9.0	6.7	4.4	6.1	6.4	4.8	
BS16(S)C2	(2)	6.1	9.4	8.9	14.6	8.5	3.5	6.4	8.2	12.6	
BS29(R)C3	(2)	5.9	6.5	8.9	9.9	5.5	6.7	8.6	7.4	6.8	
Average		7.3	8.1	9.2	13.3	6.9	5.3	7.4	8.2	10.0	
Parent mean		6.1	5.3	10.2	19.6	5.9	6.7	5.1	8.4	9.1	

† LSD<sub>(0.05)</sub> is 4.6 % for crosses and 7.0 % for parents *per se* within the crosses. Check stalk lodging mean: LH198 x LH185 = 1.9 %.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A6. Stalk lodging of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
NSS Females (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean	
	----- % -----									
BS11(FR)C14 (1)	7.4	8.0	7.8	12.9	6.9	5.5	11.0	8.5	11.8	
BS26(S)C4 (1)	7.5	11.3	12.0	17.2	7.0	6.2	6.5	9.7	14.0	
BSCB1(R)C14 (1)	6.4	6.0	4.7	13.5	3.9	3.5	5.6	6.2	4.8	
BS16(S)C2 (2)	9.0	9.8	7.1	14.2	8.3	3.6	12.1	9.2	12.6	
BS29(R)C3 (2)	5.8	7.6	5.0	7.5	9.4	8.8	8.3	7.5	6.8	
Average	7.2	8.6	7.3	13.1	7.1	5.5	8.7	8.2	10.0	
Parent mean	6.1	5.3	10.2	19.6	5.9	6.7	5.1	8.4	9.1	

† LSD<sub>(0.05)</sub> is 4.6 % for crosses and 7.0 % for parents *per se* within the crosses. Check stalk lodging mean: LH198 x LH185 = 1.9 %.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A7. Plant height of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations		SS Females (A)‡								
		----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -				
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- cm -----								
BS11(FR)C14	(1)	239.2	228.1	227.0	242.0	245.0	231.6	237.2	235.7	234.3
BS26(S)C4	(1)	237.3	236.5	231.1	241.6	246.3	238.9	232.7	237.8	238.4
BSCB1(R)C14	(1)	239.1	232.8	226.2	231.5	242.4	222.8	235.1	232.8	204.6
BS16(S)C2	(2)	229.6	226.2	221.3	226.5	229.3	216.2	225.5	224.9	209.7
BS29(R)C3	(2)	233.7	230.7	221.1	230.6	239.3	227.9	235.4	231.2	227.2
Average		235.8	230.9	225.3	234.4	240.5	227.5	233.2	232.5	222.8
Parent mean		230.8	191.3	208.0	217.4	232.6	204.9	212.2	213.9	217.6

† LSD<sub>(0.05)</sub> is 8.1 cm for crosses and 8.5 cm for parents *per se* within the crosses. Check plant height mean: LH198 x LH185 = 218.8 cm.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.



Table A8. Plant height of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----					- Adapted Exotic -- (2) -				
	NSS Females (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
----- cm -----										
BS11(FR)C14	(1)	240.5	230.5	230.1	240.2	246.2	229.5	229.7	235.2	234.3
BS26(S)C4	(1)	239.9	238.0	238.3	241.1	244.7	247.4	232.6	240.3	238.4
BSCB1(R)C14	(1)	236.3	228.6	225.8	240.1	243.9	224.8	228.1	232.5	204.6
BS16(S)C2	(2)	225.2	209.7	212.3	224.4	226.5	221.7	221.6	220.2	209.7
BS29(R)C3	(2)	236.4	229.1	224.6	239.7	250.1	231.7	233.1	235.0	227.2
Average		235.6	227.2	226.2	237.1	242.3	231.0	229.0	232.6	222.8
Parent mean		230.8	191.3	208.0	217.4	232.6	204.9	212.2	213.9	217.6

† LSD<sub>(0.05)</sub> is 8.1 cm for crosses and 8.5 cm for parents *per se* within the crosses. Check plant height mean: LH198 x LH185 = 218.8 cm.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A9. Plant ear height of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

and the 12 populations per se using combined or parent mean										
Populations		SS Females (A)‡								
		----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -				
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- cm -----								
BS11(FR)C14	(1)	117.8	105.9	110.8	116.7	118.0	112.2	112.0	113.4	108.9
BS26(S)C4	(1)	120.8	116.1	110.5	115.6	119.1	114.2	112.0	115.5	116.6
BSCB1(R)C14	(1)	112.8	107.2	104.0	106.4	108.4	100.2	109.8	107.0	87.5
BS16(S)C2	(2)	112.2	109.9	105.8	109.0	108.0	102.6	109.0	108.1	99.4
BS29(R)C3	(2)	116.8	111.2	105.3	108.5	111.6	109.7	116.7	111.4	116.0
Average		116.1	110.1	107.3	111.3	113.0	107.8	111.9	111.1	105.7
Parent mean		116.8	83.7	98.8	97.7	109.1	93.9	105.0	100.7	102.8

† LSD<sub>(0.05)</sub> is 6.7 cm for crosses and 5.9 cm for parents *per se* within the crosses. Check plant ear height mean: LH198 x LH185 = 96.6 cm.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A10. Plant ear height of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
	NSS Females (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
----- cm -----										
BS11(FR)C14	(1)	116.4	106.7	108.6	114.6	117.9	108.7	109.5	111.8	108.9
BS26(S)C4	(1)	120.5	115.2	116.9	114.6	115.7	117.7	112.3	116.1	116.6
BSCB1(R)C14	(1)	111.7	104.4	102.9	112.3	110.5	99.6	105.4	106.7	87.5
BS16(S)C2	(2)	109.2	98.0	102.6	102.9	106.0	102.1	108.9	104.3	99.4
BS29(R)C3	(2)	119.9	113.0	108.7	119.4	121.5	113.2	114.6	115.8	116.0
Average		115.5	107.5	108.0	112.8	114.3	108.3	110.1	110.9	105.7
Parent mean		116.8	83.7	98.8	97.7	109.1	93.9	105.0	100.7	102.8

† LSD<sub>(0.05)</sub> is 6.7 cm for crosses and 5.9 cm for parents *per se* within the crosses. Check plant ear height mean: LH198 x LH185 = 96.6 cm.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A11. Pollen date of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using a single environment mean.†

Populations		SS Females (A)‡								
		----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -				
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- days -----								
BS11(FR)C14	(1)	73.5	71.8	71.8	72.0	72.9	71.3	71.1	72.0	73.6
BS26(S)C4	(1)	73.1	73.9	72.1	72.4	72.8	73.0	73.5	73.0	72.2
BSCB1(R)C14	(1)	71.8	72.1	70.3	71.6	71.2	70.5	73.3	71.5	71.9
BS16(S)C2	(2)	70.4	71.2	69.7	69.5	70.5	69.3	72.0	70.4	68.5
BS29(R)C3	(2)	72.4	73.8	72.6	71.9	72.7	71.6	73.9	72.7	74.9
Average		72.2	72.6	71.3	71.5	72.0	71.1	72.7	71.9	72.2
Parent mean		73.9	74.0	72.0	71.6	73.1	70.0	72.6	72.4	72.3

† LSD<sub>(0.05)</sub> is 1.1 days for both crosses and parents *per se* within the crosses. Check days to 50% pollen shed mean: LH198 x LH185 = 71.7 days.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A12. Pollen date of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using a single environment mean.†

Populations	SS Males (A)‡									
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -					
	NSS Females (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- days -----								
BS11(FR)C14	(1)	72.3	70.1	71.9	72.7	72.5	69.8	70.8	71.4	73.6
BS26(S)C4	(1)	72.0	73.9	72.2	73.5	72.8	72.2	73.8	72.9	72.2
BSCB1(R)C14	(1)	72.0	72.1	69.8	71.0	71.1	69.8	72.0	71.1	71.9
BS16(S)C2	(2)	70.8	69.8	69.0	70.2	72.9	69.9	71.8	70.6	68.5
BS29(R)C3	(2)	72.8	72.5	71.9	73.0	73.2	72.3	73.6	72.8	74.9
Average		72.0	71.7	71.0	72.1	72.5	70.8	72.4	71.8	72.2
Parent mean		73.9	74.0	72.0	71.6	73.1	70.0	72.6	72.4	72.3

† LSD<sub>(0.05)</sub> is 1.1 days for both crosses and parents *per se* within the crosses. Check days to 50% pollen shed mean: LH198 x LH185 = 71.7 days.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A13. Silk date of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using a single environment mean.†

the 12 populations per se using a single environment mean										
Populations	SS Females (A)‡									
	----- U.S. Corn Belt -- (1)§ -----					- Adapted Exotic -- (2) -				
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- days -----								
BS11(FR)C14	(1)	74.7	73.9	73.3	73.5	72.8	73.8	73.5	73.7	74.7
BS26(S)C4	(1)	74.1	75.0	74.0	74.8	76.0	70.8	76.2	74.4	76.2
BSCB1(R)C14	(1)	73.1	74.2	71.5	72.6	73.2	72.6	76.1	73.3	73.2
BS16(S)C2	(2)	72.3	72.9	72.5	72.3	73.3	72.0	75.4	72.9	72.0
BS29(R)C3	(2)	74.7	74.8	73.7	73.8	73.9	75.5	75.5	74.6	76.4
Average		73.8	74.1	73.0	73.4	73.9	72.9	75.4	73.8	74.5
Parent mean		75.7	75.5	73.2	74.7	76.1	72.0	75.9	74.7	74.6

† LSD<sub>(0.05)</sub> is 1.2 days for both crosses and parents *per se* within the crosses. Check days to 50% silk mean: LH198 x LH185 = 72.9 days.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A14. Silk date of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using a single environment mean.†

Populations		SS Males (A)‡								
		----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -				
		----- days -----								
NSS Females (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
BS11(FR)C14	(1)	75.0	73.4	73.2	75.2	74.9	72.8	73.5	74.0	74.7
BS26(S)C4	(1)	74.3	75.1	73.9	76.0	76.4	74.8	77.8	75.5	76.2
BSCB1(R)C14	(1)	74.4	73.1	72.7	73.7	73.3	72.5	74.2	73.4	73.2
BS16(S)C2	(2)	74.5	73.2	72.2	71.8	73.6	72.5	73.6	73.1	72.0
BS29(R)C3	(2)	74.2	74.4	74.1	73.9	74.6	74.2	77.0	74.6	76.4
Average		74.5	73.8	73.2	74.1	74.5	73.4	75.2	74.1	74.5
Parent mean		75.7	75.5	73.2	74.7	76.1	72.0	75.9	74.7	74.6

† LSD<sub>(0.05)</sub> is 1.2 days for both crosses and parents *per se* within the crosses. Check days to 50% silk mean: LH198 x LH185 = 72.9 days.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table A15. Stand of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environment means.†

Population pairs using common environment means										
Populations		SS Females (A)‡								
		----- U.S. Corn Belt -- (1)§ -----					- Adapted Exotic -- (2) -			
NSS Males (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average	Parent mean
		----- p ha <sup>-1</sup> (x1000) -----								
BS11(FR)C14	(1)	59.4	59.7	59.8	59.7	58.4	59.8	59.8	59.5	59.7
BS26(S)C4	(1)	59.8	59.7	59.6	59.7	59.2	59.8	59.8	59.6	56.7
BSCB1(R)C14	(1)	59.7	59.7	59.7	59.8	59.3	59.6	59.7	59.6	59.7
BS16(S)C2	(2)	59.8	59.7	59.7	59.7	59.7	59.7	59.7	59.7	59.7
BS29(R)C3	(2)	59.8	59.7	59.7	59.8	59.7	59.8	59.8	59.7	59.7
Average		59.7	59.7	59.7	59.7	59.3	59.7	59.8	59.7	59.1
Parent mean		59.7	57.0	59.8	59.7	54.0	59.8	59.8	58.5	58.8

† LSD<sub>(0.05)</sub> is 0.7 p ha<sup>-1</sup> for crosses and 2.7 p ha<sup>-1</sup> for parents *per se* within the crosses. Check stand mean: LH198 x LH185 = 58.8 p ha<sup>-1</sup>.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.



Table A16. Stand of 35 Reciprocal  $F_1$  Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations and the 12 populations *per se* using combined environmental means.†

Populations and the 12 populations per 20 using combined environmental means.											
Populations	SS Males (A)‡								Average	Parent mean	
	----- U.S. Corn Belt -- (1)§ -----				- Adapted Exotic -- (2) -						
NSS Females (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4			
		----- p ha <sup>-1</sup> (x1000) -----									
BS11(FR)C14	(1)	59.7	59.7	59.7	59.7	59.0	59.7	59.7	59.6	59.7	
BS26(S)C4	(1)	59.7	59.7	59.7	59.8	59.6	59.7	59.7	59.7	56.7	
BSCB1(R)C14	(1)	59.7	59.7	59.8	59.7	59.7	59.8	59.8	59.7	59.7	
BS16(S)C2	(2)	59.8	59.5	59.7	59.8	59.8	59.7	59.7	59.7	59.7	
BS29(R)C3	(2)	59.7	59.7	58.5	59.7	59.7	59.8	59.6	59.5	59.7	
Average		59.7	59.7	59.5	59.7	59.6	59.7	59.7	59.7	59.1	
Parent mean		59.7	57.0	59.8	59.7	54.0	59.8	59.8	58.5	58.8	

† LSD<sub>(0.05)</sub> is 0.7 p ha<sup>-1</sup> for crosses and 2.7 p ha<sup>-1</sup> for parents *per se* within the crosses. Check stand mean: LH198 x LH185 = 58.8 p ha<sup>-1</sup>.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

**APPENDIX B**

**MEAN DIFFERENCES BETWEEN DESIGN II AND RECIPROCAL DESIGN II  
POPULATION CROSS MEANS AVERAGED OVER ENVIRONMENTS FOR  
DIFFERENT AGRONOMIC TRAITS**

Table B1. Mean difference† in grain moisture between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- % -----									
BS11(FR)C14	(1)	-0.1§	0.4	-0.5	0.6*	-0.3	0.1	0.1	0.1
BS26(S)C4	(1)	0.1	-0.3	-0.6*	-0.3	0.4	-0.5	0.1	-0.1
BSCB1(R)C14	(1)	-0.3	0.0	0.3	0.5	0.1	0.1	0.5	0.2
BS16(S)C2	(2)	0.0	0.3	-0.1	0.1	-0.2	-0.3	0.4	0.0
BS29(R)C3	(2)	0.4	0.0	-0.1	0.1	-0.5	-0.3	-0.6*	-0.2
Average		0.0	0.1	-0.2	0.2	-0.1	-0.2	0.1	0.0

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 0.3.

Table B2. Mean difference† in root lodging between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- % -----									
BS11(FR)C14	(1)	1.7§	3.9	-1.0	-0.2	-3.6	-4.9	-0.5	-0.7
BS26(S)C4	(1)	4.6	6.7	8.1	4.5	-2.7	-2.6	-2.0	2.4
BSCB1(R)C14	(1)	6.6	0.8	-4.7	7.0	1.3	1.2	-3.4	1.3
BS16(S)C2	(2)	-1.3	4.8	1.7	2.0	6.2	-1.0	4.1	2.4
BS29(R)C3	(2)	0.3	3.8	-4.5	-10.3*	4.0	-1.7	3.2	-0.7
Average		2.4	4.0	-0.1	0.6	1.0	-1.8	0.3	0.9

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 5.2.

Table B3. Mean difference† in stalk lodging between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- % -----									
BS11(FR)C14	(1)	0.8§	0.6	4.4	3.6	0.5	-0.7	-3.6	0.8
BS26(S)C4	(1)	3.6	-1.1	-3.8	-0.8	-0.5	0.7	1.8	0.0
BSCB1(R)C14	(1)	-1.3	0.0	2.9	-4.5*	2.8	0.9	0.5	0.2
BS16(S)C2	(2)	-2.9	-0.4	1.8	0.4	0.2	-0.1	-5.7*	-0.9
BS29(R)C3	(2)	0.1	-1.1	4.0	2.4	-4.0	-2.1	0.3	-0.1
Average		0.1	-0.4	1.9	0.2	-0.2	-0.3	-1.3	0.0

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 2.3.

Table B4. Mean difference† in plant height between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- cm -----									
BS11(FR)C14	(1)	-1.3§	-2.4	-3.1	1.8	-1.2	2.2	7.5	0.5
BS26(S)C4	(1)	-2.6	-1.5	-7.2	0.5	1.7	-8.5*	0.1	-2.5
BSCB1(R)C14	(1)	2.9	4.2	0.4	-8.5*	-1.5	-2.0	7.0	0.4
BS16(S)C2	(2)	4.4	16.5**	9.0*	2.1	2.8	-5.4	3.9	4.8
BS29(R)C3	(2)	-2.7	1.6	-3.4	-9.1*	-10.9**	-3.9	2.2	-3.7
Average		0.1	3.7	-0.9	-2.7	-1.8	-3.5	4.2	-0.1

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 4.1.

Table B5. Mean difference† in plant ear height between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1) ‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- cm -----									
BS11(FR)C14	(1)	1.4§	-0.8	2.2	2.1	0.1	3.5	2.6	1.6
BS26(S)C4	(1)	0.3	1.0	-6.4	1.1	3.5	-3.5	-0.2	-0.6
BSCB1(R)C14	(1)	1.1	2.8	1.1	-5.9	-2.1	0.6	4.4	0.3
BS16(S)C2	(2)	2.9	11.8**	3.2	6.1	2.0	0.6	0.1	3.8
BS29(R)C3	(2)	-3.1	-1.8	-3.5	-10.9**	-9.9**	-3.5	2.2	-4.4
Average		0.5	2.6	-0.7	-1.5	-1.3	-0.5	1.8	0.1

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 3.4.

Table B6. Mean difference† in pollen date between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using a single environment mean.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- days -----									
BS11(FR)C14	(1)	1.1§	1.8	-0.1	-0.7	0.4	1.5	0.3	0.6
BS26(S)C4	(1)	1.1	0.0	-0.1	-1.0	0.0	0.9	-0.3	0.1
BSCB1(R)C14	(1)	-0.2	0.0	0.5	0.5	0.1	0.7	1.3	0.4
BS16(S)C2	(2)	-0.4	1.3	0.7	-0.7	-2.4*	-0.7	0.2	-0.3
BS29(R)C3	(2)	-0.4	1.3	0.6	-1.1	-0.5	-0.7	0.3	-0.1
Average		0.2	0.9	0.3	-0.6	-0.5	0.3	0.3	0.2

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 1.0.



Table B7. Mean difference† in silk date between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using a single environment mean.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- days -----									
BS11(FR)C14	(1)	-0.2§	0.6	0.1	-1.8	-2.1*	1.0	0.0	-0.3
BS26(S)C4	(1)	-0.2	-0.1	0.1	-1.1	-0.4	-4.0*	-1.6	-1.1
BSCB1(R)C14	(1)	-1.3	1.1	-1.2	-1.1	-0.1	0.0	2.0	-0.1
BS16(S)C2	(2)	-2.3*	-0.3	0.2	0.4	-0.3	-0.4	1.9	-0.1
BS29(R)C3	(2)	0.5	0.4	-0.4	-0.1	-0.7	1.3	-1.6	-0.1
Average		-0.7	0.3	-0.2	-0.7	-0.7	-0.4	0.1	-0.3

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 1.0.

Table B8. Mean difference† in stand between the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses using combined environment means.

Population Crosses		Stiff-Stalk (A)							
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average
----- p ha <sup>-1</sup> (x1000) -----									
BS11(FR)C14	(1)	-0.3§	0.0	0.0	0.0	-0.6	0.0	0.0	-0.1
BS26(S)C4	(1)	0.0	0.0	-0.1	-0.1	-0.4	0.0	0.0	-0.1
BSCB1(R)C14	(1)	0.0	-0.0	-0.1	0.1	-0.5	-0.2	0.0	-0.1
BS16(S)C2	(2)	0.0	0.2	0.0	0.0	-0.1	0.0	0.0	0.0
BS29(R)C3	(2)	0.0	0.0	1.2**	0.0	0.0	0.0	0.2	0.2
Average		-0.1	0.0	0.2	0.0	-0.3	-0.0	0.0	0.0

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Population cross difference calculated as the difference between the Design II (A x B) cross and the Reciprocal Design II (B x A) cross.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

§ Standard error (SE) for mean difference between Design II (A x B) and Reciprocal Design II (B x A) population crosses is: SE = 0.4.

**APPENDIX C**

**OVERALL GENERAL COMBINING ABILITY AND SPECIFIC COMBINING  
ABILITY ESTIMATES CALCULATED OVER DESIGN II AND RECIPROCAL  
DESIGN II POPULATION CROSSES USING COMBINED ENVIRONMENT  
MEANS FOR DIFFERENT AGRONOMIC TRAITS**

Table C1. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for grain moisture averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
----- U.S. Corn Belt -- (1)‡ ----- - Adapted Exotic -- (2) -									
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Non-Stiff-Stalk GCA
----- % -----									
BS11(FR)C14	(1)	0.2*§	-0.3*	0.0	0.1	-0.1	0.0	0.1	-0.9**¶
BS26(S)C4	(1)	0.1	0.1	-0.4**	-0.2	0.1	0.1	0.2*	0.4**
BSCB1(R)C14	(1)	-0.2	-0.1	-0.2*	0.2	0.1	-0.2*	0.3**	-0.7**
BS16(S)C2	(2)	0.2	0.0	0.4**	-0.1	-0.1	0.1	-0.4**	0.1**
BS29(R)C3	(2)	-0.3**	0.3*	0.2*	0.0	0.0	0.0	-0.2	1.1**
Stiff-Stalk GCA		-0.6**#	-0.4**	0.4**	-0.2**	-0.4**	-0.2**	1.4**	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.11.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.04.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.05.

Table C2. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for root lodging averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
		----- % -----							
BS11(FR)C14	(1)	-0.3§	-1.4	1.8	-0.6	0.2	-2.9	3.3	2.0*¶
BS26(S)C4	(1)	1.8	-3.6	2.0	-2.4	1.6	2.1	-1.5	-3.0**
BSCB1(R)C14	(1)	-0.2	3.1	1.6	1.8	-3.4	-2.6	-0.2	0.8
BS16(S)C2	(2)	-0.2	0.0	-5.1**	-0.3	2.8	4.3*	-1.5	-1.9*
BS29(R)C3	(2)	-1.1	1.9	-0.2	1.6	-1.1	-0.8	-0.2	2.1*
Stiff-Stalk GCA		-1.2#	-6.0**	5.0**	-1.1	-5.7**	2.4*	6.6**	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses.  
The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 2.13.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.87.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 1.07.

Table C3. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for stalk lodging averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
		----- % -----							
BS11(FR)C14	(1)	-0.2§	-0.8	1.1	0.8	-0.5	-0.9	0.5	0.7¶
BS26(S)C4	(1)	0.6	1.0	0.4	2.2*	-1.7	-0.3	-2.1*	1.5**
BSCB1(R)C14	(1)	0.4	-0.5	-0.2	-0.0	0.2	0.4	-0.3	-1.9**
BS16(S)C2	(2)	-0.2	0.8	-0.7	0.7	0.9	-2.3*	0.8	0.5
BS29(R)C3	(2)	-0.7	-0.5	-0.5	-3.7**	1.2	3.1**	1.2	-0.7
Stiff-Stalk GCA		-1.0*#	0.1	0.0	5.0**	-1.2*	-2.8**	-0.2	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.97.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.39.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.48.

Table C4. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for plant height averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
Non-Stiff-Stalk (B)	----- U.S. Corn Belt -- (1)‡ ----- - Adapted Exotic -- (2) -								Non-Stiff-Stalk GCA
	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4		
----- cm -----									
BS11(FR)C14	(1)	1.2§	-2.6	-0.2	2.4	1.3	-1.6	-0.6	2.9**¶
BS26(S)C4	(1)	-3.6*	1.8	2.5	-0.9	-2.3	7.4**	-4.9**	6.5**
BSCB1(R)C14	(1)	1.9	1.6	0.1	-0.1	1.7	-5.5**	0.4	0.1
BS16(S)C2	(2)	1.7	-1.1	1.0	-0.3	-3.5*	-0.3	2.5	-10.0**
BS29(R)C3	(2)	-1.2	0.4	-3.5*	-1.2	2.8	0.0	2.6	0.5
Stiff-Stalk GCA		3.1**#	-3.6**	-6.8**	3.2**	8.8**	-3.3**	-1.5	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 1.70.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.69.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.85.

Table C5. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for plant ear height averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
		----- U.S. Corn Belt -- (1)‡ -----					- Adapted Exotic -- (2) -		Non-Stiff-Stalk GCA
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
----- cm -----									
BS11(FR)C14	(1)	-0.3§	-4.1**	0.5	2.1	2.7	0.9	-1.9	1.6***¶
BS26(S)C4	(1)	0.0	2.1	1.2	-1.7	-1.1	3.1*	-3.6**	4.8**
BSCB1(R)C14	(1)	0.6	1.2	-0.0	1.5	-0.1	-4.0**	0.7	-4.2**
BS16(S)C2	(2)	-0.3	0.0	1.4	-1.2	-1.9	-0.9	2.7*	-4.8**
BS29(R)C3	(2)	-0.1	0.7	-3.2*	-0.7	0.3	0.8	2.0	2.6**
Stiff-Stalk GCA		4.8***#	-2.2**	-3.4**	1.0	2.7**	-3.0**	0.0	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 1.40.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.57.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.70.



Table C6. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for pollen date averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using a single environment mean.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
		----- days -----							
BS11(FR)C14	(1)	0.9*§	-1.1**	0.8*	0.7	0.5	-0.3	-1.6**	-0.1¶
BS26(S)C4	(1)	-0.7	0.7	-0.1	0.0	-0.6	0.6	0.0	1.1**
BSCB1(R)C14	(1)	0.3	0.5	-0.6	0.0	-0.6	-0.3	0.6	-0.5**
BS16(S)C2	(2)	-0.2	-0.3	-0.4	-0.6	0.8	-0.0	0.7	-1.4**
BS29(R)C3	(2)	-0.4	0.2	0.2	-0.2	-0.2	0.1	0.3	0.9**
Stiff-Stalk GCA		0.3#	0.3	-0.7**	-0.1	0.4*	-0.9**	0.7**	0.0

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.42.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.17.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.21.

Table C7. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for silk date averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environmental means.

Stiff-Stalk (A)									

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.43.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.17.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.21.

Table C8. Overall specific combining ability (SCA) and general combining ability (GCA) estimates† for stand averaged across the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
----- U.S. Corn Belt -- (1)‡ ----- - Adapted Exotic -- (2) -									
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Non-Stiff-Stalk GCA
----- p ha <sup>-1</sup> (x1000) -----									
BS11(FR)C14	(1)	-0.1§	0.1	0.2	0.1	-0.6**	0.1	0.1	-0.1¶
BS26(S)C4	(1)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BSCB1(R)C14	(1)	0.0	0.0	0.1	-0.1	0.1	-0.1	0.0	0.0
BS16(S)C2	(2)	0.0	-0.1	0.1	0.0	0.3	-0.1	-0.1	0.1
BS29(R)C3	(2)	0.1	0.1	-0.5**	0.0	0.3*	0.1	-0.1	0.0
Stiff-Stalk GCA		0.0#	0.1	-0.1	0.1	-0.3**	0.1	0.1	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† SCA and GCA estimates presented are averaged across both the Design II (A x B) crosses and the Reciprocal Design II (B x A) crosses. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.15.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.06.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.08.

**APPENDIX D**

**RECIPROCAL CROSS GENERAL COMBINING ABILITY AND SPECIFIC  
COMBINING ABILITY ESTIMATES CALCULATED OVER DESIGN II AND  
RECIPROCAL DESIGN II POPULATION CROSSES USING COMBINED  
ENVIRONMENT MEANS FOR DIFFERENT AGRONOMIC TRAITS**

Table D1. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for grain moisture calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (NSS)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
		----- % -----							
BS11(FR)C14	(1)	-0.2§	0.3	-0.4	0.4	-0.2	0.2	0.0	0.1¶
BS26(S)C4	(1)	0.2	-0.3	-0.2	-0.4	0.6**	-0.1	0.1	-0.1
BSCB1(R)C14	(1)	-0.5*	-0.2	0.3	0.1	0.0	0.1	0.2	0.2
BS16(S)C2	(2)	0.0	0.2	0.1	-0.1	-0.2	-0.1	0.2	0.0
BS29(R)C3	(2)	0.5*	0.0	0.3	0.0	-0.2	-0.0	-0.5**	-0.1
Stiff-Stalk GCA		0.0#	0.1	-0.2	0.2*	-0.1	-0.2	0.1	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.22.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.09.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.11.

Table D2. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for root lodging calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
----- U.S. Corn Belt -- (1)‡ ----- - Adapted Exotic -- (2) -									
Non-Stiff-Stalk (NSS)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Non-Stiff-Stalk GCA	
----- % -----									
BS11(FR)C14	(1)	0.9§	1.5	0.7	0.8	-3.1	-1.5	0.8	-1.6¶
BS26(S)C4	(1)	0.8	1.3	6.7	2.5	-5.2	-2.3	-3.8	1.5
BSCB1(R)C14	(1)	3.8	-3.5	-4.9	6.0	-0.1	2.6	-4.0	0.3
BS16(S)C2	(2)	-5.1	-0.6	0.4	0.0	3.7	-0.6	2.4	1.4
BS29(R)C3	(2)	-0.4	1.4	-2.8	-9.2*	4.6	1.8	4.6	-1.7
Stiff-Stalk GCA		1.5#	3.1	-1.0	-0.3	0.1	-2.7	-0.6	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 4.27.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 1.74.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 2.13.

Table D3. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for stalk lodging calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
----- U.S. Corn Belt -- (1)‡ ----- - Adapted Exotic -- (2) -									
Non-Stiff-Stalk (NSS)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Non-Stiff-Stalk GCA	
----- % -----									
BS11(FR)C14	(1)	-0.1§	0.2	1.8	2.6	-0.1	-1.3	-3.0	0.8¶
BS26(S)C4	(1)	3.6	-0.7	-5.6**	-1.0	-0.3	1.0	3.1	0.0
BSCB1(R)C14	(1)	-1.5	0.3	0.8	-4.9**	2.8	0.9	1.6	0.2
BS16(S)C2	(2)	-2.0	1.0	0.9	1.1	1.4	1.1	-3.4	-0.9
BS29(R)C3	(2)	0.1	-0.7	2.2	2.2	-3.7*	-1.8	1.7	-0.1
Stiff-Stalk GCA		0.1#	-0.4	1.9*	0.2	-0.2	-0.3	-1.3	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 1.93.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.79.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.97.

Table D4. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for plant height calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 3.40.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 1.39.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 1.70.



Table D5. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for plant ear height calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

		Stiff-Stalk (A)							Non-Stiff-Stalk GCA
		----- U.S. Corn Belt -- (1)‡ -----				- Adapted Exotic -- (2) -			
Non-Stiff-Stalk (NSS)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	
----- cm -----									
BS11(FR)C14	(1)	-0.6§	-4.8	1.4	2.2	-0.1	2.5	-0.7	1.5¶
BS26(S)C4	(1)	0.5	-0.9	-5.0	3.3	5.5*	-2.2	-1.3	-0.8
BSCB1(R)C14	(1)	0.4	0.0	1.7	-4.5	-1.0	0.9	2.5	0.1
BS16(S)C2	(2)	-1.3	5.6*	0.2	3.9	-0.4	-2.7	-5.4	3.7**
BS29(R)C3	(2)	0.9	0.1	1.7	-4.9	-4.1	1.5	4.9	-4.5
Stiff-Stalk GCA		0.4#	2.5	-0.8	-1.7	-1.4	-0.6	1.7	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 2.81.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 1.15.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 1.40.

Table D6. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for pollen date calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using a single environment mean.

Stiff-Stalk (A)									

\*,\*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.83.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.34.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.42.

Table D7. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for silk date calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using a single environment mean.

Stiff-Stalk (A)									

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.85.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.35.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.43.

Table D8. Reciprocal cross specific combining ability (SCA) and general combining ability (GCA) estimates† for stand calculated over the 35 Design II (A x B) and 35 Reciprocal Design II (B x A) Stiff-Stalk (A) and Non-Stiff-Stalk (B) population crosses and populations *per se* using combined environment means.

Stiff-Stalk (A)									
----- U.S. Corn Belt -- (1)‡ ----- - Adapted Exotic -- (2) -									
Non-Stiff-Stalk (B)		BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Non-Stiff-Stalk GCA
----- p ha <sup>-1</sup> (x 1000) -----									
BS11(FR)C14	(1)	-0.2§	0.1	-0.1	0.1	-0.2	0.2	0.1	-0.1¶
BS26(S)C4	(1)	0.2	0.0	-0.3	0.0	0.0	0.1	0.1	-0.1
BSCB1(R)C14	(1)	0.1	0.0	-0.2	0.2	-0.1	-0.1	0.0	-0.1
BS16(S)C2	(2)	0.0	0.2	-0.2	-0.1	0.2	-0.0	-0.1	0.0
BS29(R)C3	(2)	-0.1	-0.3	0.8**	-0.2	0.1	-0.2	-0.1	0.2
Stiff-Stalk GCA		0.0#	0.1	0.2	0.0	-0.3*	0.0	0.1	0.0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Reciprocal SCA and GCA estimates calculated based on one-half of the difference between the Design II (A x B) cross and the Reciprocal Design II (A x B) cross. The first letter within parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

‡ U.S. Corn Belt and adapted exotic populations represented as (1) and (2), respectively.

§ Standard Error (SE) of Population Cross SCA: SE = 0.30.

¶ Standard Error (SE) of Non-Stiff-Stalk GCA: SE = 0.12.

# Standard Error (SE) of Stiff-Stalk GCA: SE = 0.15.

## **APPENDIX E**

**MID-PARENT HETEROSIS AND PERCENT MID-PARENT HETEROSIS  
ESTIMATES CALCULATED FOR DESIGN II AND RECIPROCAL DESIGN II  
POPULATION CROSSES USING COMBINED ENVIRONMENT MEANS FOR  
DIFFERENT AGRONOMIC TRAITS**

Table E1. Grain moisture mid-parent heterosis, expressed as the difference in percent between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----											- Adapted Exotic -- (2) -					
	NSS Males (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average
----- % -----																	
BS11(FR)C14	(1)	0.0	0	0.0	0	0.0	0	0.2	1	-0.3	-2	0.2	1	-0.3	-2	0.0	0
BS26(S)C4	(1)	0.1	1	0.1	1	-0.2	-1	-0.3	-1	0.5	2	0.3	1	0.0	0	0.1	1
BSCB1(R)C14	(1)	-0.4	-2	0.0	0	0.3	1	0.3	2	0.2	1	0.0	0	0.2	1	0.1	1
BS16(S)C2	(2)	0.0	0	0.2	1	0.6*	3	-0.1	-1	-0.2	-1	0.2	1	-0.6*	-3	0.0	0
BS29(R)C3	(2)	-0.2	-1	0.3	2	0.5	2	-0.1	-1	-0.2	-1	0.0	0	-0.8**	-4	-0.1	-1
Average		-0.1	-1	0.1	1	0.2	1	0.0	0	0.0	0	0.2	1	-0.3	-2	0.0	0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 0.25.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E2. Grain moisture mid-parent heterosis, expressed as the difference in percent between the  $F_1$  cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal  $F_1$  Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Females (B)	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
----- % -----																	
BS11(FR)C14	(1)	0.1	1	-0.5	-2	0.5**	3	-0.4	-2	0.0	0	0.2	1	-0.4	-2	-0.1	0
BS26(S)C4	(1)	0.0	0	0.4	2	0.3	2	0.0	0	0.1	1	0.7**	4	-0.1	0	0.2	1
BSCB1(R)C14	(1)	-0.1	-1	0.0	0	-0.1	-1	-0.2	-1	0.2	1	-0.1	-1	-0.3	-2	-0.1	-1
BS16(S)C2	(2)	0.0	0	-0.1	-1	0.7**	3	-0.3	-2	0.1	1	0.5	2	-1.0**	-5	0.0	0
BS29(R)C3	(2)	-0.6*	-3	0.3	2	0.5**	3	-0.1	-1	0.3	1	0.4	2	-0.3	-1	0.1	1
Average		-0.1	-1	0.0	0	0.4	2	-0.2	-1	0.1	1	0.3	2	-0.4	-2	0.0	0

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 0.25.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E3. Root lodging mid-parent heterosis, expressed as the difference in percent between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Males (B)	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
----- % -----																	
BS11(FR)C14	(1)	3.9	17	5.4	33	4.9	17	1.0	4	-1.7	-8	1.2	5	-0.2	-1	2.1	10
BS26(S)C4	(1)	7.3	40	4.4	37	9.4	39	1.3	7	-0.1	-1	7.0	38	-6.0	-18	3.3	20
BSCB1(R)C14	(1)	6.6	31	8.6	56	3.0	11	7.2	31	-2.7	-13	4.7	21	-4.9	-14	3.2	18
BS16(S)C2	(2)	1.4	7	6.1	44	-1.8	-7	1.3	6	4.6	24	9.1	44	-3.9	-11	2.4	15
BS29(R)C3	(2)	-0.1	-1	6.0	31	-1.4	-4	-4.4	-16	-1.7	-7	2.3	9	-4.5	-11	-0.5	-1
Average		3.8	19	6.1	40	2.8	11	1.3	6	-0.3	-1	4.9	23	-3.9	-11	2.1	13

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 5.39.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.



Table E4. Root lodging mid-parent heterosis, expressed as the difference in percent between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----											- Adapted Exotic -- (2) -					
	NSS Females (B)	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
----- % -----																	
BS11(FR)C14	(1)	2.2	10	1.5	9	5.9	20	1.2	5	1.9	9	6.1	26	0.3	1	2.7	11
BS26(S)C4	(1)	2.6	15	-2.4	-20	1.3	5	-3.2	-16	2.5	15	9.6	52	-4.0	-12	0.9	5
BSCB1(R)C14	(1)	0.1	1	7.8	51	7.7	28	0.2	1	-4.0	-19	3.5	16	-1.6	-4	2.0	10
BS16(S)C2	(2)	2.7	13	1.3	9	-3.5	-14	-0.7	-3	-1.6	-8	10.1	49	-8.0	-23	0.6	3
BS29(R)C3	(2)	-0.4	-2	2.3	12	3.1	10	5.9	22	-5.8	-23	4.0	15	-7.7	-19	0.2	2
Average		1.4	7	2.1	12	2.9	10	0.7	2	-1.4	-5	6.7	32	-4.2	-12	1.2	7

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 5.39.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E5. Stalk lodging mid-parent heterosis, expressed as the difference in percent between the  $F_1$  cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35  $F_1$  Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.<sup>†</sup>

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Males (B)	BS10(FR)C14	BS13(S)C9	BSK(HI)C11	BSK(S)C11	BSSS(R)C14	BS28(R)C3	BS34(S)C4	Average								
	----- % -----																
BS11(FR)C14	(1)	-0.9	-9	0.0	0	1.2	11	0.8	5	-1.5	-17	-4.5	-48	-1.0	-12	-0.8	-10
BS26(S)C4	(1)	1.1	11	0.6	6	-3.9	-32	-0.3	-2	-3.5	-35	-3.4	-33	-1.2	-13	-1.5	-14
BSCB1(R)C14	(1)	-0.3	-6	1.0	20	0.1	1	-3.2	-26	1.3	25	-1.4	-24	1.2	25	-0.2	-2
BS16(S)C2	(2)	-3.3	-35	0.5	5	-2.5	-22	-1.5	-9	-0.8	-8	-6.1**	-63	-2.4	-27	-2.3	-23
BS29(R)C3	(2)	-0.6	-9	0.5	8	0.4	5	-3.3	-25	-0.9	-13	0.0	0	2.7	45	-0.2	-2
Average		-0.8	-10	0.5	8	-1.0	-8	-1.5	-12	-1.0	-10	-3.1	-34	-0.2	4	-1.0	-9

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

<sup>†</sup> Standard error (SE) of mid-parent heterosis; SE = 2.36.

<sup>‡</sup> The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

<sup>§</sup> U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E6. Stalk lodging mid-parent heterosis, expressed as the difference in percent between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Females (B)	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
	----- % -----																
BS11(FR)C14	(1)	-1.6	-18	-0.5	-6	-3.2	-29	-2.9	-18	-2.0	-22	-3.7	-40	2.6	30	-1.6	-15
BS26(S)C4	(1)	-2.6	-26	1.7	18	-0.1	-1	0.4	2	-2.9	-30	-4.2	-40	-3.0	-32	-1.5	-15
BSCB1(R)C14	(1)	1.0	17	1.0	20	-2.8	-37	1.3	11	-1.5	-27	-2.3	-39	0.7	14	-0.4	-6
BS16(S)C2	(2)	-0.4	-4	0.9	10	-4.3	-38	-2.0	-12	-1.0	-11	-6.0**	-62	3.3	37	-1.4	-11
BS29(R)C3	(2)	-0.7	-11	1.6	27	-3.5	-42	-5.7*	-43	3.1	49	2.1	31	2.4	40	-0.1	-7
Average		-0.9	-8	0.9	14	-2.8	-29	-1.8	-12	-0.9	-8	-2.8	-30	1.2	18	-1.0	-8

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 2.36.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E7. Plant height mid-parent heterosis, expressed as the difference in centimeters between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across three environments.†

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average		
NSS Males (B)		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%
BS11(FR)C14	(1)	6.6	3	15.3**	7	5.8	3	16.2**	7	11.6**	5	12.0**	5	14.0**	6	11.6**	5
BS26(S)C4	(1)	2.7	1	21.7**	10	7.9*	4	13.7**	6	10.9**	5	17.2**	8	7.4*	3	11.6**	5
BSCB1(R)C14	(1)	21.5**	10	34.9**	18	19.9**	10	20.5**	10	23.8**	11	18.1**	9	26.7**	13	23.6**	11
BS16(S)C2	(2)	9.4**	4	25.7**	13	12.4**	6	13.0**	6	8.1*	4	9.0**	4	14.6**	7	13.2**	6
BS29(R)C3	(2)	4.7	2	21.5**	10	3.5	2	8.3**	4	9.4**	4	11.8**	5	15.7**	7	10.7**	5
Average		9.0*	4	23.8**	12	9.9**	5	14.3**	7	12.7**	6	13.6**	6	15.7**	7	14.2**	7

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 2.81.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E8. Plant height mid-parent heterosis, expressed as the difference in centimeters between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across three environments.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average		
NSS Females (B)		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%
BS11(FR)C14	(1)	7.9*	3	17.7**	8	9.0*	4	14.4**	6	12.8**	5	9.9**	5	6.4*	3	11.1**	5
BS26(S)C4	(1)	5.3	2	23.2**	11	15.1**	7	13.3**	6	9.2*	4	25.7**	12	7.3*	3	14.2**	6
BSCB1(R)C14	(1)	18.6**	9	30.7**	15	19.5**	9	29.1**	14	25.3**	12	20.1**	10	19.7**	9	23.3**	11
BS16(S)C2	(2)	5.0	2	9.2*	5	3.5	2	10.9**	5	5.4	2	14.4**	7	10.7**	5	8.4*	4
BS29(R)C3	(2)	7.4*	3	19.9**	10	7.0	3	17.4**	8	20.2**	9	15.7**	7	13.4**	6	14.4**	7
Average		8.8*	4	20.1**	10	10.8**	5	17.0**	8	14.6**	6	17.2**	8	11.5**	5	14.3**	7

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 3.61.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E9. Plant ear height mid-parent heterosis, expressed as the difference in centimeters between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across three environments.†

Populations		SS Females (A)‡															
		----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -					
		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
NSS Males (B)		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%
BS11(FR)C14	(1)	5.0	4	9.6**	10	7.0*	7	13.5**	13	9.0**	8	10.8**	11	5.1	5	8.6**	8
BS26(S)C4	(1)	4.1	3	16.0**	16	2.8	3	8.5**	8	6.3*	6	9.0**	9	1.3	1	6.9*	6
BSCB1(R)C14	(1)	10.6**	10	21.6**	25	10.9**	12	13.8**	15	10.1**	10	9.4**	10	13.5**	14	12.9**	14
BS16(S)C2	(2)	4.1	4	18.3**	20	6.7*	7	10.5**	11	3.8	4	6.0*	6	6.8*	7	8.0**	8
BS29(R)C3	(2)	0.4	0	11.3**	11	-2.1	-2	1.7	2	-0.9	-1	4.8	5	6.3*	6	3.1	3
Average		4.8	4	15.4**	16	5.1	5	9.6**	10	5.7*	5	8.0**	8	6.6*	6	7.9**	8

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 2.81.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E10. Plant ear height mid-parent heterosis, expressed as the difference in centimeters between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across three environments.†

Populations		SS Males (A)‡															
		----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -					
		NSS Females (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4	
		cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%	cm	%
BS11(FR)C14	(1)	3.6	3	10.4**	11	4.8	5	11.4**	11	8.9**	8	7.3**	7	2.6	2	7.0*	7
BS26(S)C4	(1)	3.8	3	15.0**	15	9.2**	9	7.5**	7	2.8	3	12.5**	12	1.6	1	7.5**	7
BSCB1(R)C14	(1)	9.5**	9	18.8**	22	9.7**	10	19.7**	21	12.2**	12	8.9**	10	9.2**	10	12.6**	14
BS16(S)C2	(2)	1.2	1	6.5*	7	3.6	4	4.4	4	1.8	2	5.4	6	6.7*	7	4.2	4
BS29(R)C3	(2)	3.5	3	13.2**	13	1.4	1	12.6**	12	8.9**	8	8.3**	8	4.1	4	7.4**	7
Average		4.3	4	12.8**	14	5.7*	6	11.1**	11	6.9*	7	8.5**	8	4.8	5	7.7**	8

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 2.81.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E11. Pollen date mid-parent heterosis, expressed as the difference in days between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations using a single environment mean.†

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Males (B)	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
		days	%	days	%	days	%	days	%	days	%	days	%	days	%	days	%
BS11(FR)C14	(1)	-0.3	0	-1.9	-3	-1.0	-1	-0.6	-1	-0.4	-1	-0.5	-1	-2.0	-3	-1.0	-1
BS26(S)C4	(1)	0.1	0	0.8	1	0.0	0	0.5	1	0.2	0	2.0	3	1.1	1	0.7	1
BSCB1(R)C14	(1)	-1.0	-1	-0.8	-1	-1.6	-2	-0.2	0	-1.3	-2	-0.4	-1	1.1	1	-0.6	-1
BS16(S)C2	(2)	-0.8	-1	-0.1	0	-0.6	-1	-0.6	-1	-0.3	0	0.0	0	1.5	2	-0.1	0
BS29(R)C3	(2)	-2.0	-3	-0.6	-1	-0.9	-1	-1.3	-2	-1.3	-2	-0.9	-1	0.1	0	-1.0	-1
Average		-0.8	-1	-0.5	-1	-0.8	-1	-0.4	-1	-0.6	-1	0.0	0	0.3	0	-0.4	-1

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 1.04.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.



Table E12. Pollen date mid-parent heterosis, expressed as the difference in days between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations using a single environment mean.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Females (B)	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average	
		days	%	days	%	days	%	days	%	days	%	days	%	days	%	days	%
BS11(FR)C14	(1)	-1.4	-2	-3.7**	-5	-0.9	-1	0.1	0	-0.9	-1	-2.0	-3	-2.3*	-3	-1.6	-2
BS26(S)C4	(1)	-1.0	-1	0.8	1	0.1	0	1.6	2	0.2	0	1.1	2	1.4	2	0.6	1
BSCB1(R)C14	(1)	-0.8	-1	-0.8	-1	-2.2*	-3	-0.7	-1	-1.4	-2	-1.2	-2	-0.2	0	-1.0	-1
BS16(S)C2	(2)	-0.4	0	-1.4	-2	-1.2	-2	0.1	0	2.1*	3	0.7	1	1.3	2	0.2	0
BS29(R)C3	(2)	-1.6	-2	-1.9	-3	-1.5	-2	-0.3	0	-0.8	-1	-0.1	0	-0.2	0	-0.9	-1
Average		-1.1	-1	-1.4	-2	-1.1	-2	0.2	0	-0.1	0	-0.3	0	0.0	0	-0.6	-1

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 1.04.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E13. Silk date mid-parent heterosis, expressed as the difference in days between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 F<sub>1</sub> Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations using a single environment mean.

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Males (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average
		days	%	days	%	days	%	days	%	days	%	days	%	days	%	days	%
BS11(FR)C14	(1)	-0.4	-1	-1.2	-2	-0.7	-1	-1.2	-2	-2.6*	-3	0.5	1	-1.8	-2	-1.0	-1
BS26(S)C4	(1)	-1.8	-2	-0.9	-1	-0.7	-1	-0.6	-1	-0.1	0	-3.3**	-4	0.2	0	-1.0	-1
BSCB1(R)C14	(1)	-1.4	-2	-0.2	0	-1.7	-2	-1.4	-2	-1.5	-2	0.0	0	1.6	2	-0.7	-1
BS16(S)C2	(2)	-1.6	-2	-0.9	-1	-0.1	0	-1.1	-1	-0.8	-1	0.0	0	1.5	2	-0.4	-1
BS29(R)C3	(2)	-1.4	-2	-1.2	-2	-1.1	-1	-1.7	-2	-2.4*	-3	1.3	2	-0.7	-1	-1.0	-1
Average		-1.3	-2	-0.9	-1	-0.8	-1	-1.2	-2	-1.5	-2	-0.3	0	0.1	0	-0.8	-1

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 1.02.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E14. Silk date mid-parent heterosis, expressed as the difference in days between the F<sub>1</sub> cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal F<sub>1</sub> Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations using a single environment mean.

Non-Sun Stalk (NSS) populations using a single environment model																	
Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----											- Adapted Exotic -- (2) -					
	NSS Females (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average
		days	%	days	%	days	%	days	%	days	%	days	%	days	%	days	%
BS11(FR)C14	(1)	-0.2	0	-1.7	-2	-0.8	-1	0.6	1	-0.5	-1	-0.5	-1	-1.8	-2	-0.7	-1
BS26(S)C4	(1)	-1.6	-2	-0.7	-1	-0.7	-1	0.5	1	0.3	0	0.7	1	1.8	2	0.0	0
BSCB1(R)C14	(1)	0.1	0	-1.3	-2	-0.5	-1	-0.3	0	-1.4	-2	-0.1	0	-0.4	0	-0.6	-1
BS16(S)C2	(2)	0.7	1	-0.6	-1	-0.4	0	-1.5	-2	-0.5	-1	0.5	1	-0.4	0	-0.3	0
BS29(R)C3	(2)	-1.8	-2	-1.5	-2	-0.7	-1	-1.7	-2	-1.7	-2	0.1	0	0.8	1	-0.9	-1
Average		-0.6	-1	-1.2	-2	-0.6	-1	-0.5	-1	-0.8	-1	0.1	0	0.0	0	-0.5	-1

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 1.02.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

Table E15. Stand mid-parent heterosis, expressed as the difference in  $p\ ha^{-1}$  between the  $F_1$  cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35  $F_1$  Design II (A x B) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Females (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average		
NSS Males (B)		p ha <sup>-1</sup> ¶	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%
BS11(FR)C14	(1)	-0.4	0	1.3	2	0.0	0	0.0	0	1.6	3	0.0	0	0.1	0	0.4	1
BS26(S)C4	(1)	1.6	3	2.9**	5	1.4	2	1.5	3	3.9**	7	1.5	3	1.5	3	2.0*	4
BSCB1(R)C14	(1)	0.0	0	1.3	2	0.0	0	0.1	0	2.4*	4	-0.2	0	0.0	0	0.5	1
BS16(S)C2	(2)	0.0	0	1.4	2	0.0	0	0.0	0	2.8**	5	-0.1	0	0.0	0	0.6	1
BS29(R)C3	(2)	0.0	0	1.4	2	0.0	0	0.0	0	2.9**	5	0.0	0	0.0	0	0.6	1
Average		0.2	0	1.7	3	0.3	0	0.3	1	2.7**	5	0.3	0	0.3	0	0.8	1

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 0.97.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

¶ Stand is expressed in  $p\ ha^{-1}$  in 1000<sup>th</sup> of an hectare.

Table E16. Stand mid-parent heterosis, expressed as the difference in  $p\ ha^{-1}$  between the  $F_1$  cross and the mid-parent value, and percent mid-parent heterosis, expressed as a percent by division of the mid-parent heterosis value by the mid-parent value and multiplying by 100, of 35 Reciprocal  $F_1$  Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations combined across six environments.†

Populations	SS Males (A)‡																
	----- U.S. Corn Belt -- (1)§ -----										- Adapted Exotic -- (2) -						
	NSS Females (B)		BS10(FR)C14		BS13(S)C9		BSK(HI)C11		BSK(S)C11		BSSS(R)C14		BS28(R)C3		BS34(S)C4		Average
		p ha <sup>-1</sup> ¶	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%	p ha <sup>-1</sup>	%
BS11(FR)C14	(1)	-0.1	0	1.4	2	0.0	0	0.0	0	2.1*	4	0.0	0	0.0	0	0.5	1
BS26(S)C4	(1)	1.5	3	2.9**	5	1.5	3	1.6	3	4.3**	8	1.5	3	1.5	3	2.1*	4
BSCB1(R)C14	(1)	0.0	0	1.4	2	0.1	0	-0.1	0	2.9**	5	0.0	0	0.0	0	0.6	1
BS16(S)C2	(2)	0.1	0	1.1	2	0.0	0	0.1	0	2.9**	5	-0.1	0	0.0	0	0.6	1
BS29(R)C3	(2)	0.0	0	1.4	2	-1.2	-2	0.0	0	2.9**	5	0.0	0	-0.2	0	0.4	1
Average		0.3	1	1.6	3	0.1	0	0.3	1	3.0**	5	0.3	0	0.3	0	0.8	1

\*, \*\* Significantly different from zero at the 0.05 and 0.01 significance levels.

† Standard error (SE) of mid-parent heterosis; SE = 0.97.

‡ The Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations are designated as (A) and (B). The first letter within the parentheses listed above (i.e., (A x B) or (B x A)) serves as the female parent in the cross.

§ U.S. Corn Belt and adapted exotic populations denoted as (1) and (2), respectively.

¶ Stand is expressed in  $p\ ha^{-1}$  in 1000<sup>th</sup> of an hectare.

**APPENDIX F**

**INDIVIDUAL ENTRY MEANS AVERAGED OVER ENVIRONMENTS FOR  
DIFFERENT AGRONOMIC TRAITS**

Table F1. Mean performance of all entries from experiment 20 averaged across environments in 2002.

Entry No.†	Pedigree‡	YIELD§ (t ha <sup>-1</sup> )	STAND (p ha <sup>-1</sup> )	MOIST	RTL DG ----- % -----	SKLDG	PLTHT¶ --- cm ---	EARHT#	POLDT†† --- days ---	SILK
1	BS10(FR)C14/BS11(FR)C14	7.68	59.4	18.5	26.7	8.1	239.2	117.8	73.5	74.7
2	BS11(FR)C14/BS10(FR)C14	7.44	59.7	18.6	25.0	7.4	240.5	116.4	72.3	75.0
3	BS10(FR)C14/BS26(S)C4	7.24	59.8	19.8	25.4	11.1	237.3	120.8	73.1	74.1
4	BS26(S)C4/BS10(FR)C14	7.24	59.7	19.7	20.8	7.5	239.9	120.5	72.0	74.3
5	BS10(FR)C14/BS29(R)C3	8.03	59.8	20.2	25.4	5.9	233.7	116.8	72.4	74.7
6	BS29(R)C3/BS10(FR)C14	7.89	59.7	19.9	25.1	5.8	236.4	119.9	72.8	74.2
7	BS10(FR)C14/BSCB1(R)C14	7.60	59.7	18.2	28.1	5.2	239.1	112.8	71.8	73.1
8	BSCB1(R)C14/BS10(FR)C14	7.41	59.7	18.5	21.6	6.4	236.3	111.7	72.0	74.4
9	BS10(FR)C14/BS16(S)C2	7.18	59.8	19.5	21.5	6.1	229.6	112.2	70.4	72.3
10	BS16(S)C2/BS10(FR)C14	6.89	59.8	19.5	22.8	9.0	225.2	109.2	70.8	74.5
11	BS34(S)C4/BS11(FR)C14	6.59	59.8	20.4	37.1	7.4	237.2	112.0	71.1	73.5
12	BS11(FR)C14/BS34(S)C4	7.09	59.8	20.3	37.5	11.0	229.7	109.5	70.8	73.5
13	BS34(S)C4/BS26(S)C4	5.47	59.8	21.9	26.5	8.3	232.7	112.1	73.5	76.2
14	BS26(S)C4/BS34(S)C4	5.67	59.7	21.8	28.5	6.5	232.6	112.3	73.8	77.8
15	BS34(S)C4/BS29(R)C3	6.23	59.8	21.9	35.5	8.6	235.4	116.7	73.9	75.5
16	BS29(R)C3/BS34(S)C4	6.22	59.6	22.4	32.3	8.3	233.1	114.6	73.6	77.0
17	BS34(S)C4/BSCB1(R)C14	6.34	59.7	21.1	31.0	6.1	235.1	109.8	73.3	76.1
18	BSCB1(R)C14/BS34(S)C4	5.95	59.8	20.6	34.3	5.6	228.1	105.4	72.0	74.2
19	BS34(S)C4/BS16(S)C2	5.74	59.7	21.1	30.7	6.4	225.5	109.0	72.0	75.4
20	BS16(S)C2/BS34(S)C4	5.41	59.7	20.7	26.6	12.1	221.6	108.9	71.8	73.6

† Entry number of genotypes evaluated in experiment 20 in 2002.

‡ Pedigree of crosses listed with female parent first.

§ YIELD, STAND, MOIST (grain moisture), RTL DG (root lodging), and SKLDG (stalk lodging) measured on all plants in all environments.

¶ PLTHT (plant height) measured from the soil surface to the terminal node. Mean averaged across three environments.

# EARHT (ear height) measured from the soil surface to the upper ear shank node. Mean averaged across three environments.

†† POLDT (pollen date) and SILK (silk date) equal days from planting when the plant showed male and female anthesis, respectively.

Table F1. (cont.)

Entry No.	Pedigree	YIELD	STAND	MOIST	RTLDG	SKLDG	PLTHT	EARHT	POLDT	SILK
21	BS28(R)C3/BS11(FR)C14	7.38	59.8	18.7	24.4	4.8	231.6	112.2	71.3	73.8
22	BS11(FR)C14/BS28(R)C3	6.68	59.7	18.7	29.3	5.5	229.5	108.7	69.8	72.8
23	BS28(R)C3/BS26(S)C4	6.58	59.8	20.0	25.6	6.9	238.9	114.2	73.0	70.8
24	BS26(S)C4/BS28(R)C3	6.41	59.7	20.4	28.2	6.2	247.4	117.7	72.2	74.8
25	BS28(R)C3/BS29(R)C3	6.34	59.8	20.5	28.3	6.7	227.9	109.7	71.6	75.5
26	BS29(R)C3/BS28(R)C3	6.23	59.8	20.9	30.0	8.8	231.7	113.2	72.3	74.2
27	BS28(R)C3/BSCB1(R)C14	6.93	59.6	18.7	26.7	4.4	222.8	100.2	70.5	72.6
28	BSCB1(R)C14/BS28(R)C3	6.96	59.8	18.6	25.5	3.5	224.8	99.6	69.8	72.5
29	BS28(R)C3/BS16(S)C2	6.13	59.7	19.7	29.7	3.5	216.2	102.6	69.3	72.0
30	BS16(S)C2/BS28(R)C3	6.20	59.7	20.0	30.7	3.6	221.7	102.1	69.9	72.5
31	BSSS(R)C14/BS11(FR)C14	7.39	58.4	18.2	20.1	7.4	245.0	118.0	72.9	72.8
32	BS11(FR)C14/BSSS(R)C14	7.68	59.0	18.5	23.7	6.9	246.2	117.9	72.5	74.9
33	BSSS(R)C14/BS26(S)C4	7.51	59.2	20.1	17.0	6.5	246.3	119.1	72.8	76.0
34	BS26(S)C4/BSSS(R)C14	7.35	59.6	19.8	19.7	7.0	244.7	115.7	72.8	76.4
35	BSSS(R)C14/BS29(R)C3	7.91	59.7	20.3	22.8	5.5	239.3	111.6	72.7	73.9
36	BS29(R)C3/BSSS(R)C14	7.92	59.7	20.8	18.8	9.4	250.1	121.5	73.2	74.6
37	BSSS(R)C14/BSCB1(R)C14	7.53	59.3	18.9	17.8	6.7	242.4	108.4	71.2	73.2
38	BSCB1(R)C14/BSSS(R)C14	8.04	59.7	18.8	16.5	3.9	243.9	110.5	71.1	73.3
39	BSSS(R)C14/BS16(S)C2	6.96	59.7	19.4	23.7	8.5	229.3	108.0	70.5	73.3
40	BS16(S)C2/BSSS(R)C14	7.33	59.8	19.6	17.6	8.3	226.5	106.0	72.9	73.6
41	BS13(S)C9/BS11(FR)C14	7.40	59.7	18.4	22.0	8.6	228.1	105.9	71.8	73.9
42	BS11(FR)C14/BS13(S)C9	8.00	59.7	18.0	18.1	8.0	230.5	106.7	70.1	73.4
43	BS13(S)C9/BS26(S)C4	7.32	59.7	19.8	16.2	10.2	236.5	116.1	73.9	75.0
44	BS26(S)C4/BS13(S)C9	7.44	59.7	20.1	9.5	11.3	238.0	115.2	73.9	75.1
45	BS13(S)C9/BS29(R)C3	7.43	59.7	20.8	25.3	6.5	230.7	111.2	73.8	74.8
46	BS29(R)C3/BS13(S)C9	7.82	59.7	20.8	21.5	7.6	229.1	113.0	72.5	74.4



Table F1. (cont.)

Entry No.	Pedigree	YIELD	STAND	MOIST	RTLDTG	SKLDG	PLTHT	EARHT	POLDT	SILK
47	BS13(S)C9/BSCB1(R)C14	7.58	59.7	18.7	23.8	6.0	232.8	107.2	72.1	74.2
48	BSCB1(R)C14/BS13(S)C9	7.86	59.7	18.6	23.0	6.0	228.6	104.4	72.1	73.1
49	BS13(S)C9/BS16(S)C2	6.78	59.7	19.6	20.0	9.4	226.2	109.9	71.2	72.9
50	BS16(S)C2/BS13(S)C9	7.34	59.5	19.3	15.2	9.8	209.7	98.0	69.8	73.2
51	BSK(S)C11/BS11(FR)C14	7.07	59.7	19.1	25.6	16.5	242.0	116.7	72.0	73.5
52	BS11(FR)C14/BSK(S)C11	7.49	59.7	18.4	25.8	12.9	240.2	114.6	72.7	75.2
53	BSK(S)C11/BS26(S)C4	6.27	59.7	19.7	21.2	16.5	241.6	115.6	72.4	74.8
54	BS26(S)C4/BSK(S)C11	6.09	59.8	20.0	16.7	17.2	241.1	114.6	73.5	76.0
55	BSK(S)C11/BS29(R)C3	6.77	59.8	20.8	22.9	9.9	230.6	108.5	71.9	73.8
56	BS29(R)C3/BSK(S)C11	7.10	59.7	20.7	33.2	7.5	239.7	119.4	73.0	73.9
57	BSK(S)C11/BSCB1(R)C14	6.94	59.8	19.3	30.5	9.0	231.5	106.4	71.6	72.6
58	BSCB1(R)C14/BSK(S)C11	6.53	59.7	18.8	23.5	13.5	240.1	112.3	71.0	73.7
59	BSK(S)C11/BS16(S)C2	6.61	59.7	19.7	23.2	14.6	226.5	109.0	69.5	72.3
60	BS16(S)C2/BSK(S)C11	6.56	59.8	19.6	21.2	14.2	224.4	102.9	70.2	71.8
61	BSK(HI)C11/BS11(FR)C14	7.23	59.8	19.1	33.7	12.2	227.0	110.8	71.8	73.3
62	BS11(FR)C14/BSK(HI)C11	7.05	59.7	19.6	34.7	7.8	230.1	108.6	71.9	73.2
63	BSK(HI)C11/BS26(S)C4	6.38	59.6	20.0	33.5	8.2	231.1	110.5	72.1	74.0
64	BS26(S)C4/BSK(HI)C11	6.71	59.7	20.5	25.4	12.0	238.3	116.9	72.2	73.9
65	BSK(HI)C11/BS29(R)C3	6.60	59.7	21.5	30.1	8.9	221.1	105.3	72.6	73.7
66	BS29(R)C3/BSK(HI)C11	7.10	58.5	21.6	34.6	5.0	224.6	108.7	71.9	74.1
67	BSK(HI)C11/BSCB1(R)C14	6.96	59.7	19.4	30.5	7.6	226.2	104.0	70.3	71.5
68	BSCB1(R)C14/BSK(HI)C11	7.13	59.8	19.1	35.2	4.7	225.8	102.9	69.8	72.7
69	BSK(HI)C11/BS16(S)C2	6.46	59.7	20.7	24.3	8.9	221.3	105.8	69.7	72.5
70	BS16(S)C2/BSK(HI)C11	6.65	59.7	20.7	22.6	7.1	212.3	102.6	69.0	72.2
71	BS10(FR)C14	6.77	59.7	18.9	18.3	6.1	230.8	116.8	73.9	75.7
72	BS34(S)C4	4.10	59.8	23.4	47.1	5.1	212.2	105.0	72.6	75.9

Table F1. (cont.)

Entry No.	Pedigree	YIELD	STAND	MOIST	RTLDG	SKLDG	PLTHT	EARHT	POLDT	SILK
73	BS28(R)C3	4.96	59.8	18.9	19.2	6.7	204.9	93.9	70.0	72.0
74	BSSS(R)C14	4.86	54.0	18.9	16.3	5.9	232.6	109.1	73.1	76.1
75	BS13(S)C9	5.26	57.0	18.8	5.8	5.3	191.3	83.7	74.0	75.5
76	BSK(S)C11	5.19	59.7	19.6	21.8	19.6	217.4	97.7	71.6	74.7
77	BSK(HI)C11	5.32	59.8	20.0	30.3	10.2	208.0	98.8	72.0	73.2
78	BS11(FR)C14	5.83	59.7	18.1	27.3	11.8	234.3	108.9	73.6	74.7
79	BS26(S)C4	5.16	56.7	20.4	17.9	14.0	238.4	116.6	72.2	76.2
80	BS29(R)C3	5.80	59.7	22.0	32.8	6.8	227.2	116.0	74.9	76.4
81	BSCB1(R)C14	3.87	59.7	18.4	24.7	4.8	204.6	87.5	71.9	73.2
82	BS16(S)C2	5.07	59.7	20.1	21.9	12.6	209.7	99.4	68.5	72.0
83	BSSSC0	3.56	58.9	18.6	31.4	19.3	232.3	115.6	72.0	76.2
84	BSCB1C0	4.10	59.8	18.1	24.9	19.8	222.0	106.4	70.1	73.5
85	BS10C0	4.59	58.4	18.5	24.1	16.8	222.3	111.6	71.8	75.2
86	BS11C0	4.32	59.8	21.6	34.2	14.0	241.7	134.2	73.5	80.2
87	BSKC0	2.53	43.4	19.3	46.0	15.2	228.2	117.6	74.0	77.1
88	BS26C0	4.82	41.2	20.0	30.8	12.7	233.6	108.6	72.4	74.5
89	LH198/LH185	9.66	58.8	17.8	16.9	1.9	218.8	96.9	71.7	72.9
90	DK595	9.45	59.7	17.3	8.3	3.3	231.9	99.5	72.1	72.7
91	BS22(R)C7	4.94	58.8	17.4	20.3	3.9	194.3	87.6	64.8	68.2
92	BS21(R)C7	4.70	59.8	16.9	7.4	9.4	190.1	86.3	64.8	67.7
93	BS21(R)C7/BS22(R)C7	6.12	59.8	17.5	14.3	5.0	199.9	88.7	64.8	66.8
94	TEPR-EC6	4.71	59.6	16.8	26.1	11.4	188.3	81.7	66.5	67.1

Table F1. (cont.)

Entry No.	Pedigree	YIELD	STAND	MOIST	RTLDTG	SKLDG	PLTHT	EARHT	POLDT	SILK
95	BS11(30-S1)C8	6.31	59.7	19.7	15.3	5.3	222.6	100.0	71.6	73.8
96	BS11(20-S1)C8	5.41	59.3	19.5	16.1	5.6	209.6	99.4	72.0	73.8
97	BS11(S2)C5	6.09	59.7	20.3	28.9	8.3	234.1	117.0	74.4	76.1
98	BS31(R)C1	6.42	59.8	21.3	26.5	6.8	236.8	118.4	74.0	75.3
99	RX740	10.34	59.1	18.4	22.1	2.7	233.8	107.1	75.6	76.6
100	GH2547	9.88	59.7	18.8	18.8	2.5	213.7	96.3	71.3	72.6
	Experiment Minimum	2.53	41.2	16.8	5.8	1.9	188.3	81.7	64.8	66.8
	Experiment Maximum	10.34	59.8	23.4	47.1	19.8	250.1	134.2	75.6	80.2
	Experiment Mean	6.57	59.2	19.6	24.8	8.5	228.5	108.8	71.7	73.9
	LSD(0.05)‡‡	0.59	1.8	0.6	11.4	4.9	9.1	6.7	1.1	1.0
	EEMS§§	0.15	0.8	0.1	46.9	13.5	22.1	15.0	0.5	0.5

‡‡ Least significant difference at 0.05 significance level.

§§ Effective error mean squares.

## **APPENDIX G**

### **SUMS OF SQUARES EQUATIONS FOR PARTITIONED CROSS EFFECTS FOR A DESIGN II ANALYSIS**

Design II (A x B) Crosses							Reciprocal Design II (B x A) Crosses						
NSS males (B)	SS Females (A)					$x_{.Bj}$	NSS Females (B)	SS males (A)					$r_{.Bj}$
	1	2	3	4	5			1	2	3	4	5	
6	$x_{16}$	$x_{26}$	$x_{36}$	$x_{46}$	$x_{56}$	$x_{.6}$	6	$r_{16}$	$r_{26}$	$r_{36}$	$r_{46}$	$r_{56}$	$r_{.6}$
7	$x_{17}$	$x_{27}$	$x_{37}$	$x_{47}$	$x_{57}$	$x_{.7}$	7	$r_{17}$	$r_{27}$	$r_{37}$	$r_{47}$	$r_{57}$	$r_{.7}$
8	$x_{18}$	$x_{28}$	$x_{38}$	$x_{48}$	$x_{58}$	$x_{.8}$	8	$r_{18}$	$r_{28}$	$r_{38}$	$r_{48}$	$r_{58}$	$r_{.8}$
9	$x_{19}$	$x_{29}$	$x_{39}$	$x_{49}$	$x_{59}$	$x_{.9}$	9	$r_{19}$	$r_{29}$	$r_{39}$	$r_{49}$	$r_{59}$	$r_{.9}$
$x_{Ai.}$	$x_{1.}$	$x_{2.}$	$x_{3.}$	$x_{4.}$	$x_{5.}$	$x_{..}$	$r_{Ai.}$	$r_{1.}$	$r_{2.}$	$r_{3.}$	$r_{4.}$	$r_{5.}$	$r_{..}$

Figure G1. Mating design setup for partitioned population cross effects between Design II (A x B) crosses and Reciprocal Design II (B x A) crosses between Stiff-Stalk (SS) and Non-Stiff-Stalk (NSS) populations.

Sums of squares for population cross partitions between Design II (A x B) crosses and Reciprocal Design II (B x A) crosses. Above example shows simplified designs with reduced number of females and males compared to the actual number used within the experiment. Overall sums of squares effects consider both types of design crosses, while reciprocal sums of squares effects consider the difference between the two types of design crosses.

Sums of Squares Estimation for Overall effects:

$$\text{Stiff-Stalk SS's} = \sum_{Ai=1}^5 \left( \frac{(\overline{X_{Ai.}} + \overline{R_{Ai.}})}{2} - \frac{(\overline{X_{..}} + \overline{R_{..}})}{2} \right)^2$$

$$\text{Non-Stiff-Stalk SS's} = \sum_{Bj=1}^4 \left( \frac{(\overline{X_{.Bj}} + \overline{R_{.Bj}})}{2} - \frac{(\overline{X_{..}} + \overline{R_{..}})}{2} \right)^2$$

$$\text{Overall SS x NSS Interaction} = \sum_{Ai=1}^5 \sum_{Bj=1}^4 \left[ \left( \frac{(\overline{X_{ij}} + \overline{R_{ij}})}{2} \right) - \left( \frac{(\overline{X_{Ai.}} + \overline{R_{Ai.}})}{2} \right) - \left( \frac{(\overline{X_{.Bj}} + \overline{R_{.Bj}})}{2} \right) + \left( \frac{(\overline{X_{..}} + \overline{R_{..}})}{2} \right) \right]^2$$

Sums of Squares Estimation for Reciprocal effects:

$$\text{Stiff-Stalk (maternal) SS's} = \sum_{Ai=1}^5 \left( \frac{(\overline{X_{Ai.}} - \overline{R_{Ai.}})}{2} \right)^2$$

$$\text{Non-Stiff-Stalk (maternal) SS's} = \sum_{Bj=1}^4 \left( \frac{(\overline{X_{.Bj}} - \overline{R_{.Bj}})}{2} \right)^2$$

$$\text{Reciprocal SS x NSS Interaction} = \sum_{Ai=1}^5 \sum_{Bj=1}^4 \left[ \left( \frac{(\overline{X_{ij}} - \overline{R_{ij}})}{2} \right) - \left( \frac{(\overline{X_{Ai.}} - \overline{R_{Ai.}})}{2} \right) - \left( \frac{(\overline{X_{.Bj}} - \overline{R_{.Bj}})}{2} \right) + \left( \frac{(\overline{X_{..}} - \overline{R_{..}})}{2} \right) \right]^2$$

Sums of Squares Estimation for a second analysis identifying only the Reciprocal Effect:

$$\text{Reciprocal Effect} = \sum_{Ai=1}^5 \sum_{Bj=1}^4 \left[ \left( \frac{(\overline{X_{ij}} - \overline{R_{ij}})}{2} \right) \right]^2$$

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